CALIFORNIA FISH AND GAME

"CONSERVATION THROUGH EDUCATION"

VOLUME 88 FALL 2002 NUMBER 4

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CALIFORNIA FISH AND GAME

VOLUME 88 FALL 2002 NUMBER 4

Published Quarterly by

STATE OF CALIFORNIA
THE RESOURCES AGENCY
DEPARTMENT OF FISH AND GAME
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California Fish and Game 88(4):149-164 2002

LARVAL DELTA SMELT DIET COMPOSITION AND FEEDING INCIDENCE: ENVIRONMENTAL AND ONTOGENETIC INFLUENCES

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I examined the feeding ecology of larval delta smelt, *Hypomesus transpacificus*, a threatened fish endemic to the upper San Francisco Estuary (SFE). The larvae were collected during California Department of Fish and Game ichthyoplankton surveys during spring 1992-1994. The study objectives were (1) compare current diet composition to limited historical data; (2) describe seasonal and ontogenetic influences on the diet; and (3) determine whether feeding success varied interannually, and if so, in association with what factors. In most months, historically important prey, (cyclopid copepods and the calanoid copepod *Eurytemora affinis*) dominated the diet. The calanoid copepod *Pseudodiaptomus forbesi*, introduced to the SFE in 1987, was an important prey in late spring. Electivity analysis indicated use of the aforementioned copepods was related to their abundance, but changes in the abundance of other zooplankton were not reflected in the diet. Ontogenetic changes in the size of prey ingested were apparent; the smallest feeding larvae ate mostly subadult copepods, whereas larvae ≥ 13 mm ate mostly adult copepods. Feeding incidence (FI), the presence or absence of food in the gut, increased with larval length, but for certain length groups varied up to 30% among years. A Separate Slopes Analysis of Covariance (ANCOVA) indicated larval length was positively correlated with Principal Components scores representing a gradient in calanoid copepod abundance. The ANCOVA also demonstrated that on average, feeding larvae were collected in association with higher calanoid copepod abundance than equivalently sized non-feeding larvae. Overall these results suggest (1) larval delta smelt are primarily dependent on three prey taxa, two of which have undergone a long-term decline in abundance, and (2) larval delta smelt feeding success is related to prey abundance. I conclude that well-documented ecological changes in the SFE have probably been detrimental to larval delta smelt, but that linking long-term or interannual food web variability to recruitment will require further research.

INTRODUCTION

Delta smelt, *Hypomesus transpacificus*, is a small, pelagic, estuarine-dependent fish endemic to the upper San Francisco Estuary including the Sacramento-San Joaquin

Delta (Moyle et al. 1992). Delta smelt is a State and federally listed threatened species, which underwent a substantial population decline beginning in the early 1980s (Sweetnam 1999). Although its adult abundance has recovered somewhat in recent years, it continues to show depressed juvenile abundances relative to abundance levels recorded in the 1970s. The factors affecting delta smelt recruitment are not well understood, but estuarine hydrology, water diversions, food web alterations, exotic species, and contaminants have all been implicated (Bennett and Moyle 1996).

The low salinity zone (LSZ) of the upper estuary has historically been an important rearing area for several fishes, including delta smelt (Moyle et al. 1992; Bennett and Moyle 1996). Long-term declines in productivity at several trophic levels have occurred in the approximately 0.5‰-6.0‰ LSZ (Lehman 1992; Kimmerer and Orsi 1996; Kimmerer et al. 2000). In addition to long-term declines in productivity, substantial changes to the LSZ ecosystem occurred following the introduction of a filter-feeding clam *Potamocorbula amurensis* in 1986 (Nichols et al. 1990). The establishment of *P. amurensis* was associated with substantial declines in phytoplankton (Alpine and Cloern 1992), the calanoid copepod, *Eurytemora affinis*, (Kimmerer et al. 1994) and the mysid *Neomysis mercedis* (Orsi and Mecum 1996). Spatial and temporal changes in plankton dynamics also occurred following the *P. amurensis* introduction. The abundance maxima of diatoms (Lehman 2000) and *E. affinis* (Kimmerer and Orsi 1996), which historically occurred in the LSZ, shifted into tidal fresh water regions. In addition, *E. affinis*, which historically was abundant through the summer, has been replaced system-wide each May or June by *Pseudodiaptomus forbesi*, a calanoid copepod introduced in 1987 (Kimmerer and Orsi 1996). These changes in LSZ plankton dynamics have been considered detrimental to young striped bass, *Morone saxatilis* (Meng and Orsi 1991; Kimmerer et al. 2001). They may also have been detrimental to delta smelt since limited historical diet data indicate *E. affinis* was the principal prey (Moyle et al. 1992).

Lack of detailed diet data for larval delta smelt, and information on other aspects of its feeding ecology limit current understanding of the potential impacts of food web alterations. This study investigates the feeding ecology of larval delta smelt in years following the *P. amurensis* introduction through exploratory analysis of 3 years of larval fish, zooplankton, and physical monitoring data. Specifically, I focused on three questions. (1) Has the diet changed since the latter 1970s? (2) What are the seasonal and ontogenetic influences on diet composition? (3) Does feeding success vary interannually, and if so, can environmental influences on feeding success be discerned?

METHODS

Field Methods For Collection Of Larval Fish And Zooplankton

Larval delta smelt were collected during 1992-1994 by the California Department of Fish and Game (CDFG) Egg and Larval Survey (ELS). The ELS was developed to concurrently monitor the distribution and abundance of larval striped bass and

zooplankton (CDFG[1] 1987), but larval delta smelt were commonly collected incidentally. The ELS samples were taken every 2-4 days at 60-80 stations throughout Suisun Bay and the Sacramento-San Joaquin Delta (Wang[2] 1991). Sampling encompassed most of the known range of delta smelt. The ELS samples were collected with a 505-μm mesh plankton net (0.5 m^2 mouth) mounted on a sled and towed obliquely from bottom to surface for 10 minutes at each station. Most samples were collected between sunrise and early afternoon. The volume of water that passed through the net was estimated with a General Oceanics™ flow meter. Zooplankton was usually sampled simultaneously with a 154-μm mesh Clarke-Bumpus (CB) net attached to the sled above the ELS net. A second General Oceanics™ flow meter estimated the volume of water that passed through the CB net. Water temperature (°C), surface specific conductance (microsiemens/cm), and water clarity (Secchi disk depth, m) were also recorded at each station. All samples were preserved in 5% buffered formalin. Larval delta smelt and zooplankton were identified in the laboratory by CDFG staff. This dataset contrasted a year of above average freshwater flow conditions (1993), with 2 years of below average flow conditions (1992 and 1994) (California Department of Water Resources[3] unpublished data for 1906-1999). Hereafter, 1993 is referred to as 'wet' and 1992 and 1994 are referred to as 'dry'.

Gut Contents Analysis

Larval delta smelt collected during April and May 1992 (n = 208) and March through June, 1993-1994 (n = 529 and 737, respectively) were randomly subsampled from ELS collections for gut content analysis. Standard length (SL) of each larva was measured to the nearest 0.1 mm using a dissecting microscope with an ocular micrometer. The definition of larva in this paper corresponds to the prolarva through prejuvenile stages of Wang[2] (1991). The maximum SL included in the analysis was 20.4 mm. For larvae collected in 1994, mouth widths were measured to the nearest 0.1 mm and related to SL using linear regression. The contents of the entire digestive tracts were identified and counted. Whenever possible, I identified all post-naupliar copepods and non-copepod zooplankton to genus. Because most copepod genera are monospecific in the freshwater and low salinity habitats of the upper estuary (Kimmerer and Orsi 1996),

[1]CDFG (California Department of Fish and Game). 1987. Factors affecting striped bass abundance in the Sacramento-San Joaquin River system, Exhibit 25, entered by the California Department of Fish and Game for the State Water Resources Control Board 1987 Water Quality/Water Rights Proceeding on the San Francisco Bay and Sacramento-San Joaquin Delta. Interagency Ecological Program for the Sacramento-San Joaquin Estuary Technical Report 20.

[2]Wang, J.C.S. 1991. Early life stages and early life history of the delta smelt, *Hypomesus transpacificus*, in the Sacramento-San Joaquin Estuary, with comparison of early life stages of the longfin smelt, *Spirinchus thaleichthys*. Interagency Ecological Studies Program for the Sacramento-San Joaquin Estuary Technical Report 28.

[3]CDWR (California Department of Water Resources). Raw data are available at http://cdec.water.ca.gov/cgi-progs/iodir/wsihist

identifications to genus refer to particular species and are reported as such in this paper. The zooplankton collected in the CB samples were identified according to a slightly different protocol. In the CB samples, only adult copepods were identified to genus. Sub-adult copepodite stages were identified to order (Calanoida, Cyclopoida, or Harpacticoida). Zooplankton and physical environment data, taken concurrently with smelt larvae, were available for 1,021 (69%) of the larvae examined for gut contents.

DATA ANALYSIS

All diet composition data reported in this paper were summarized as percentages of prey occurrence by number (%N). To allow differentiation between seasonal and ontogenetic influences on the diet, I summarized larval SL and %N in two ways. In the first, I calculated mean SL and %N for each month each year. In the second, I calculated %N for each 1 mm SL increment between 5 and 20 mm. The latter summary was based on combined data for all 3 years.

To assess prey use versus potential prey availability, I calculated Vanderploeg-Scavia electivity indices (Lechowicz 1982) for each fish meeting the following criteria: (1) the fish was collected with a concurrent CB zooplankton sample, and (2) the fish had eaten only prey taxa that were quantitatively sampled with the CB net. A total of 301 larvae met these criteria. The index was calculated as:

$E^* = [W_i - (1/n)]/[W_i + (1/n)]$
where
$W_i = (r_i/p_i)/(\Sigma r_i/p_i)$
and
r_i = relative abundance of a prey category in the diet
p_i = relative abundance of a prey category in the environment
n = number of prey categories considered.

Electivity indices are problematic when used on field data because they assume all prey types were present in every sample (Lechowicz 1982). When each prey type is not present, the index for that prey type has a mathematically nonsensical denominator of zero. Of the 301 fish included in the analysis, only 3 had eaten a prey type that was not observed in the simultaneous environment sample. These fish were excluded from further analysis. In cases where a prey item was not found in either the gut contents or the environment, the electivity index was set to zero and the fish were included in subsequent analyses because zero electivity was expected at zero abundance.

Appropriate diet data were grouped into six prey categories for the electivity analysis (Table 1). After calculating an electivity index for each larva for each prey category, I paired each electivity index for each prey category with its concurrent abundance estimate (number/m^3) from the field. Then I ranked the pairs lowest to highest based on the field abundance estimates. Next each pair was assigned to one of three bins of approximately equal sample size (Table 1). I tested the null hypotheses that there were no differences in electivity between abundance bins for each of the six

Table 1. Prey taxa and their ranges of abundance (organisms/m³) in each abundance bin used in the analysis of larval delta smelt electivity.

Prey Taxon	Bin 1 (n = 100)	Bin 2 (n = 99)	Bin 3 (n = 99)
Total cyclopidae	0 – 149	149 – 528	534 – 16,612
Cal. copepodites	0 – 1,482	1,482 – 3,415	3,415 – 17,448
E. affinis adults	0 – 216	216 – 999	999 – 3,415
P. forbesi adults	0 – 103	107 – 649	649 – 10,702
S. doerri adults	0 – 234	244 – 640	640 – 6,581
Total cladocera	0 – 141	141 – 980	980 – 84,871

prey categories using Kruskal-Wallis nonparametric analyses of variance. To correct for the increased possibility of type I errors given six hypothesis tests, I used a Dunn-Sidak adjusted P-value to support or refute the null hypotheses (Sokal and Rohlf 1995). The adjusted α needed to reject the null hypotheses was 0.009.

I used feeding incidence (FI), the presence or absence of food items in the gut, as an index of larval feeding success (Dauvin and Dodson 1990). Based on studies of other larval fishes (Hunter 1981; Gerking 1994; Bremigan and Stein 1997), I expected FI to vary with size of the larvae and with environmental conditions. As an initial assessment of these assumptions, I assigned each larva that had a simultaneous environment sample (n = 1,021) to 1 of 5 bins of approximately equal sample size (n = 204-205) based on SL. The number of bins was arbitrary, but designed to balance between retaining large sample sizes and not masking trends by being overly inclusive. Based on a qualitative examination of FI among years and SL bins, statistical examination of environmental conditions and their interaction with SL was warranted.

Since FI is a binary variable, I used a logistic regression approach (generalized linear model with binomial distribution and logit link function) to test for factors that contributed significantly to FI. The aforementioned SL bins were used as a categorical variable in the logistic analysis. In addition, I natural log transformed and standardized the physical environment data and the abundance data for zooplankton taxa that had shown a significant electivity response. These data were summarized using Principal Components Analysis (PCA) to produce a reduced number of independent variables. The constant 10 was added to each zooplankton abundance estimate before natural log transformation to avoid taking a log of zero. The logistic model comprised a Separate Slopes Analysis of Covariance (ANCOVA); [FI = (SL bin X PC1 scores) + (SL bin X PC2 scores) + SL bin]. Model coefficients were considered statistically significant at α = 0.05.

RESULTS

In each year, the mean SL of the delta smelt larvae increased throughout the spring (Table 2). Copepods of various life stages predominated in the diet in all months, always accounting for > 85% of the gut contents. The most commonly eaten copepods

Table 2. Monthly summaries of sample sizes used for diet analysis of larval delta smelt, monthly means and standard deviations of delta smelt standard length, and monthly diet composition as percent numeric contribution, 1992-1994.

	1992		1993				1994			
	April	May	March	April	May	June	March	April	May	June
# guts examined	114	94	132	146	237	14	143	481	90	23
mean standard length (mm)	6.8	11.2	5.9	7.3	8.6	11.3	5.6	7.1	11.3	15.6
Std. Dev. of SL (mm)	2.7	4.3	1.2	2.2	4.2	3.9	0.6	2.1	4.5	3.6
Diet composition										
Total Copepoda	97.8	95.3	85.5	95.8	97.9	92.6	97.5	98.4	100	100
Copepod nauplii	22.2	6.0	53.2	11.5	12.6	56.9	60.0	35.2	12.3	0
Harpacticoida	4.4	0	0	0	0	0	5.0	5.1	1.5	0
Cyclopoida										
Cyclopidae	15.6	1.3	29.0	54.2	8.5	6.5	25.0	14.3	3.6	0.8
Oithonidae	0	0	0	0	0	0	0	0.2	0	0
Calanoida										
Eurytemora affinis										
adults	4.4	6.0	1.6	2.7	43.2	0	0	6.4	52.8	20.8
copepodites	0	5.3	0	21.4	25.4	0	0	9.2	11.8	0
Pseudodiaptomus forbesi										
adults	0	42.7	0	0	0.8	11.4	0	0	5.1	59.2
copepodites	0	6.0	0	0	1.9	14.6	0	0	1.0	18.3

Sinocalanus doerrii										
adults	0	2.7	0	1.1	0.3	0	0	0	2.6	0
copepodites	0	0	0	0.4	0	0	0	0.2	0.5	0.8
Osphranticum										
labronectum	0	0	0	0	0	0	0	0.2	0	0
Diaptomus spp.	0	0	1.6	0.4	0	0	0	0	0	0
unidentified										
calanoid copepods[a]	51.1	25.3	0	4.2	5.2	3.3	7.5	27.8	8.7	0
Non-copepod zooplankton										
cladocera	0	0.7	0	1.1	0.5	4.1	0	0.5	0	0
rotifera	2.2	4.0	14.5	3.1	1.6	3.3	2.5	0.9	0	0
chironomid larvae	0	0	0	0	0	0	0	0.2	0	0
Estimated contributions[b]										
Cyclopidae + *E. affinis*										
all life stages	77.0	18.0	81.2	92.9	93.5	16.8	65.0	73.7	85.4	21.6
cyclopidae + *E. affinis* + *P. forbesi*										
all life stages	77.0	89.6	81.3	92.9	96.8	87.5	65.0	73.7	93.1	99.1

[a]represents both early copepodite stages that could not be identified to genus and, rarely, later copepodite and adult stages of individuals that were digested beyond recognition.
[b]estimates based on assumption that nauplii and unidentified calanoids had the same taxonomic composition as the identified copepods, cyclopidae, *E. affinis* and *P. forbesi*, respectively

represented different life stages of three taxa: cyclopidae, *Eurytemora affinis* and *Pseudodiaptomus forbesi*. Collectively, these taxa represented an estimated 65% to 99% of monthly diet composition. The prey category 'nauplii' included the larval stages of both calanoid and cyclopid copepods, but the proportions of each were not determined. The prey category 'unidentified calanoids' included individuals which were badly digested, but more often, it represented morphologically similar early copepodite stages that were difficult to differentiate. Since virtually all of the calanoid copepodites that could be identified to genus or species were *E. affinis* or *P. forbesi*, most of the unidentified calanoids were probably *E. affinis* and *P. forbesi* as well.

Seasonal shifts in diet were apparent (Table 2). Cyclopids were most commonly eaten in March-April, whereas *E. affinis* was most commonly eaten in April-May, and *P. forbesi* in May-June. Interannual differences in diet composition were also apparent. *P. forbesi* contributed to the diet more in 1992 than the other years. Similarly, cyclopids were more important in 1993 than other years. Other apparent seasonal shifts in diet (e.g., nauplii) were due to ontogenetic changes in the size of prey consumed rather than to season per se (Fig. 1). Nauplii, which are the small larval stages of copepods, and other small zooplankters such as harpacticoid and oithonid copepods, and rotifers were principally eaten by the smallest feeding larvae (5-8 mm). In contrast, the larger adult copepods were principally eaten by delta smelt $\geq$ 13 mm. The increase in prey size with length was consistent with a gradual increase in mouth width as SL increased [mouth width $= 0.082(SL) + 0.0016$; $r^2 = 0.89$; $P < 0.001$; df $= 595$].

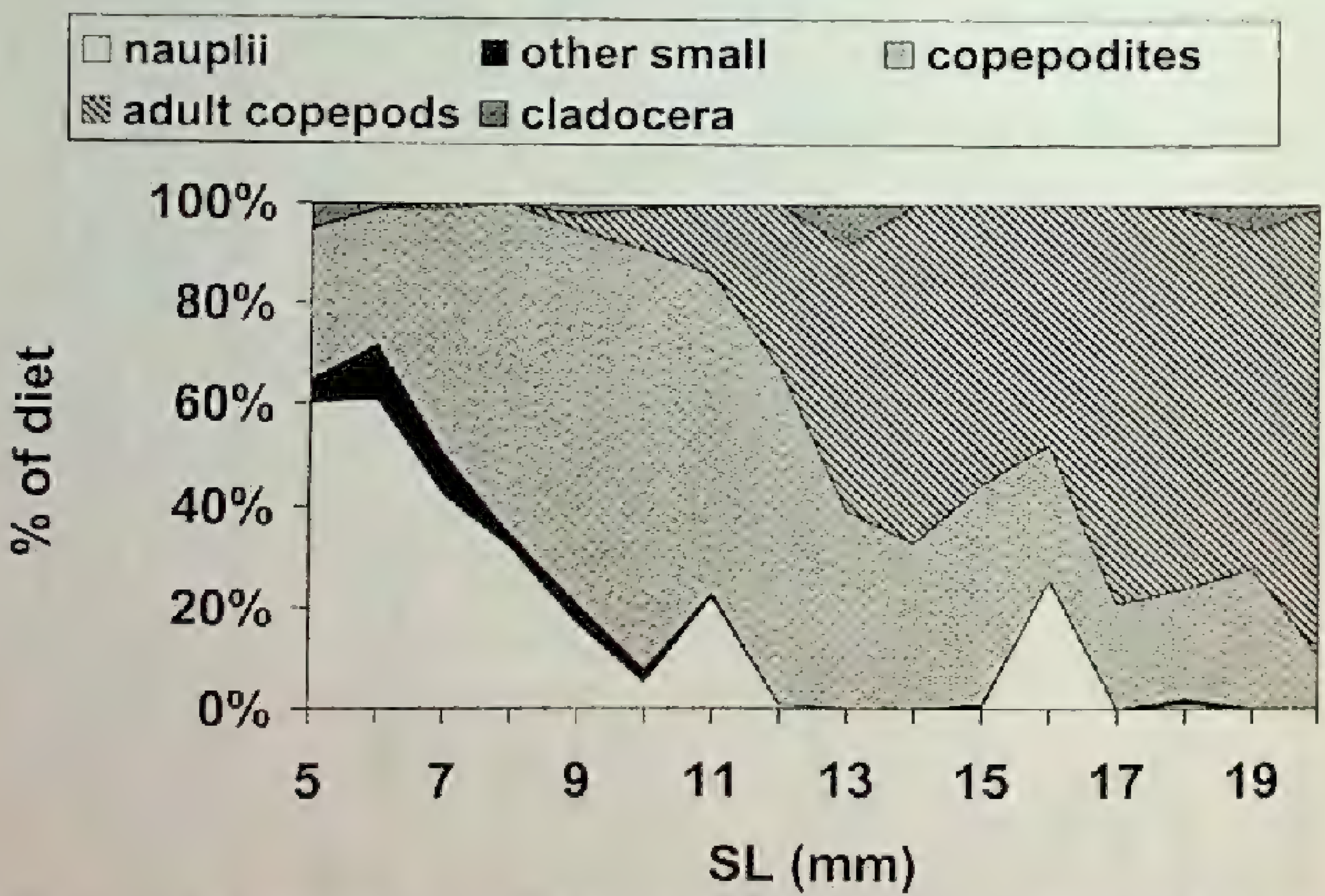

Figure 1. Larval delta smelt diet composition (% by number of occurrences) versus larval delta smelt standard length for each 1 mm length group between 5 and 20 mm.

The electivity analysis indicated larval delta smelt feed on a subset of potentially available prey types, and that prey use was influenced by changes in prey abundance (Fig. 2). Larval delta smelt significantly increased their use of cyclopids, calanoid copepodites, and adult *E. affinis* and *P. forbesi* as the abundance of these prey increased (all $P < 0.0001$). In contrast, use of *S. doerri* ($P > 0.07$) and cladocerans ($P > 0.37$) did not increase in accordance with abundance in the environment.

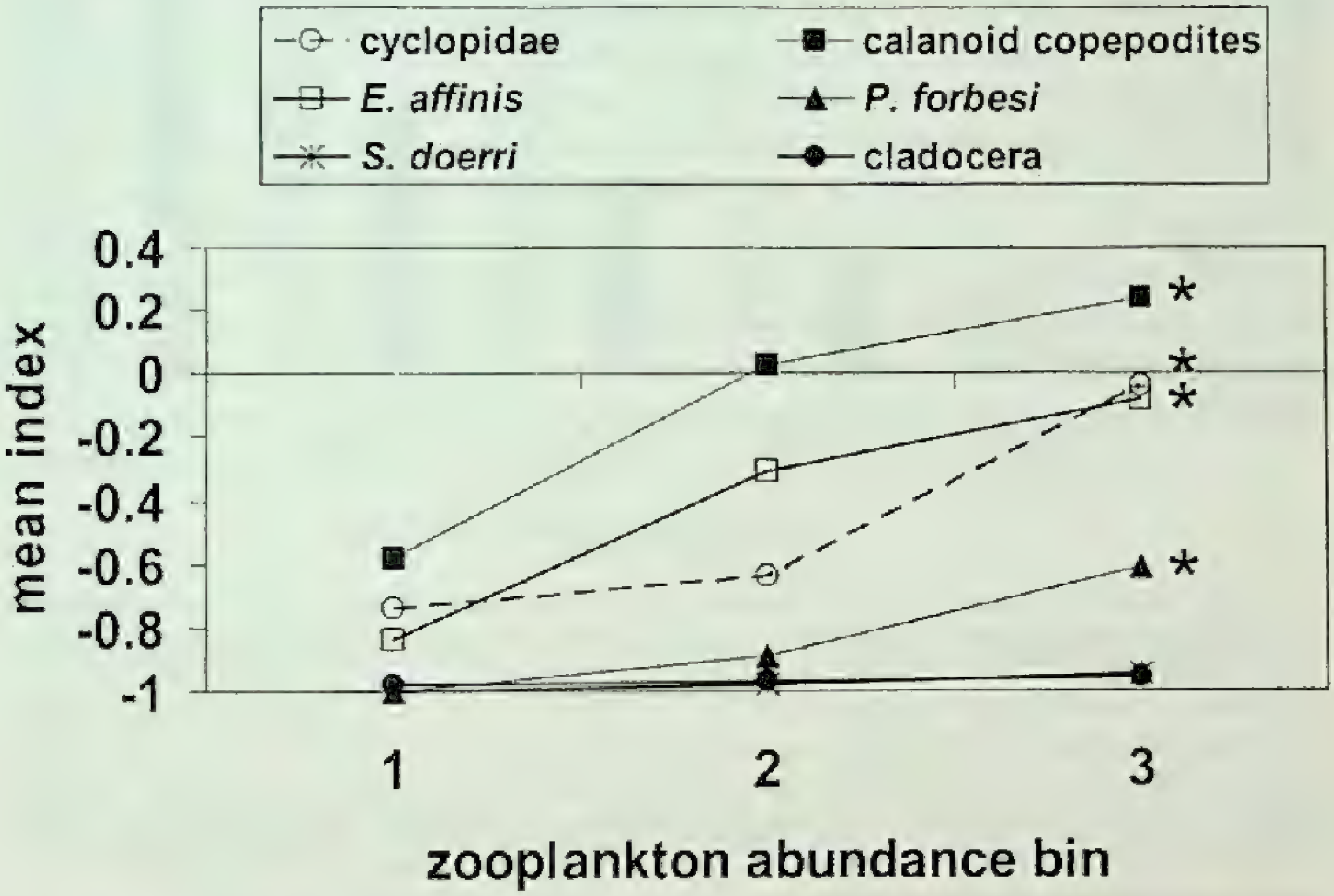

Figure 2. Relationship between bins of zooplankton abundance (number/m^3) and mean electivity for each zooplankton group shown by concurrently collected larval delta smelt. Bin 1 included the lowest 100 abundance estimates, bin 2 the intermediate 99 abundance estimates, and bin 3 the highest 99 abundance estimates for each zooplankton group. The asterisks denote changes in mean electivity that Kruskal-Wallis analyses of variance indicated were statistically significant at a Dunn-Sidak adjusted significance level of $\alpha < 0.009$.

Larval delta smelt FI varied with both SL and year of collection (Fig. 3). Overall, SL had a much larger influence than year of collection. However, interannual differences in FI were substantial (up to about 30%) within SL bins 3 and 4 (6.1 to 9.8 mm larvae) suggesting variation in environmental conditions can substantially affect feeding success of larvae shortly after the onset of exogenous feeding. Between 1992 and 1994, the ELS recorded a considerable range of environmental conditions (Table 3). For the most part, larval delta smelt were collected over much of the range of, and under similar mean conditions to, those recorded for the entire survey. Notable exceptions were that on average larval delta smelt were collected from locations where specific conductance

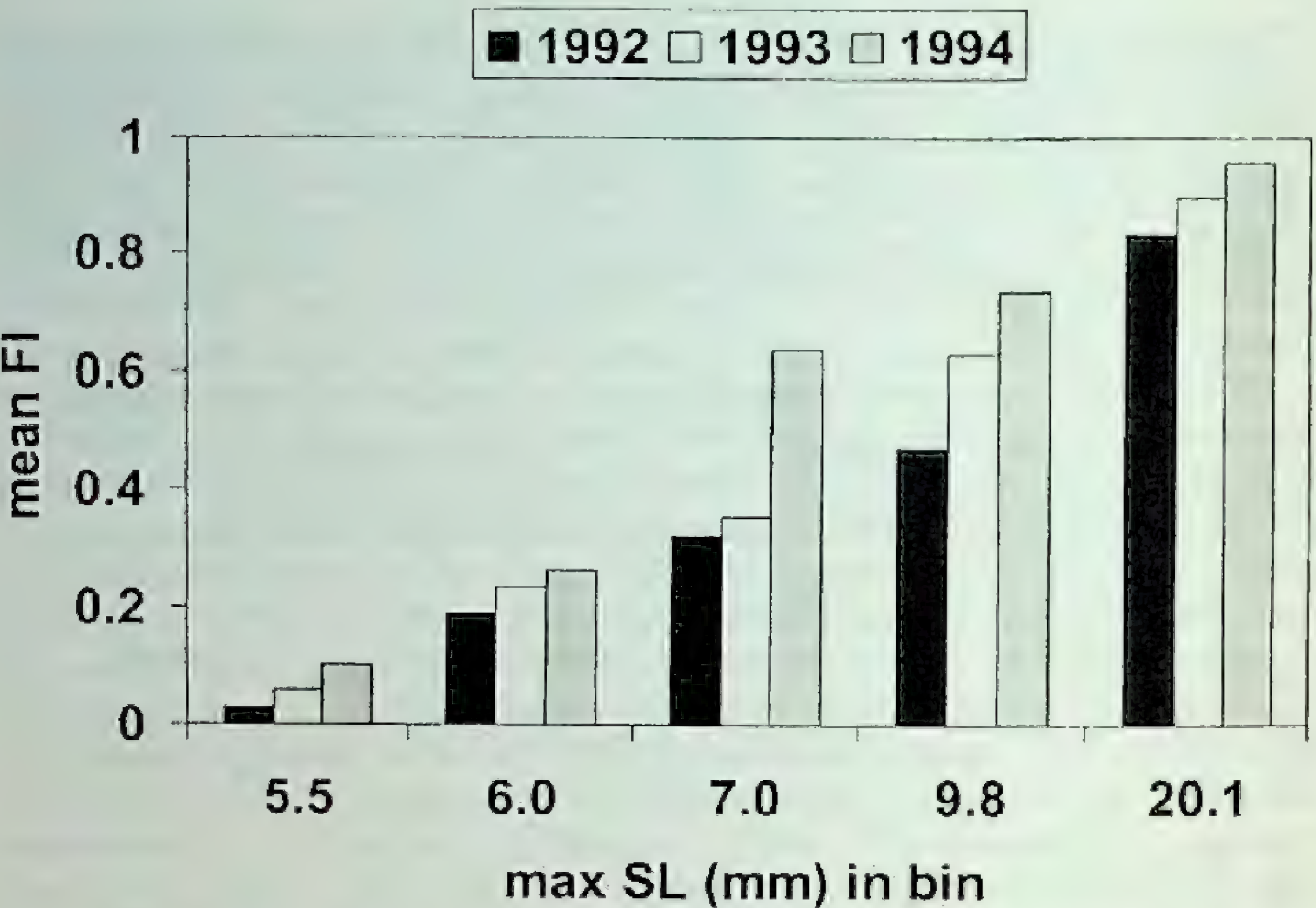

Figure 3. Larval delta smelt feeding incidence (FI; the proportion of larvae with food in their gut) versus standard length (mm), 1992-1994. Each SL bin included 204-205 fish. The minimum length in bin 1 was 4.0 mm.

Table 3. Means and ranges of environmental variables measured during the California Department of Fish and Game Egg and Larval Survey (ELS), means and ranges of ELS environmental variables for the subset of ELS data based on measurements taken concurrently with larval delta smelt collections April-May 1992 and March-June 1993-1994, and Principal Components Analysis loadings of the ln-transformed and standardized ELS environmental variables taken concurrently with larval delta smelt collections. PC1 had an eigenvalue of 3.99 and explained 50% of the variance in environmental conditions. PC2 had an eigenvalue of 1.32 and explained 16% of the variance in environmental conditions.

Environmental variable	ELS mean (range)	Smelt mean (range)	PC1	PC2
Water temperature (°C)	17.6 (10.3 - 27.2)	16.8 (10.6 - 23.3)	0.63	-0.37
Secchi disk depth (m)	0.51 (0.05 - 1.6)	0.55 (0.15 - 1.5)	0.03	-0.92
Surf. conductivity (µs/cm)	1,901 (72 - 27,088)	454 (82 - 7,913)	0.63	0.55
Copepod nauplii (#/m^3)	622 (0 - 50,207)	644 (0 - 31,246)	0.84	0.04
Cyclopid copepodites (#/m^3)	531 (0 - 36,609)	605 (0 - 12,484)	-0.57	0.20
Calanoid copepodites (#/m^3)	1,627 (0 - 30,698)	1,684 (0 - 17,448)	0.89	-0.02
E. affinis adults (#/m^3)	191 (0 - 6,008)	321 (0 - 3,414)	0.84	0.002
P. forbesi adults (#/m^3)	721 (0 - 40,214)	432 (0 - 10,702)	0.82	0.01

was an order of magnitude lower than the average for the entire survey. In addition, maximum water temperature and copepod abundances for the entire survey were somewhat higher than the maxima where delta smelt larvae were collected.

The PCA produced two principal components (PC) with eigenvalues > 1 (Table 3); the first PC explained 50% of the variation in the environmental variables, and the second PC explained an additional 16% of the variation. The PC1 represented a gradient in calanoid copepod abundance because nauplii, calanoid copepodites, *E. affinis* adults, and *P. forbesi* adults all had loadings onto PC1 that were > 0.80. Surface specific conductance and water temperature also loaded onto PC1, but less strongly than the correlated calanoid copepod variables. A fifth copepod abundance variable, total cyclopidae, contrasted somewhat with the other copepod variables. The PC2 primarily represented a gradient in Secchi disk depth that separated wet year conditions (positive PC2 scores) from the dry year conditions (negative PC2 scores).

In the ANCOVA, the SL bin and SL bin X PC1 terms were significantly positively correlated with FI (Table 4). The SL X PC2 term was not correlated with FI. Larger larvae co-occurred with higher abundances of calanoid copepods than smaller larvae (Fig. 4). However, feeding larvae in each SL bin were collected in association with higher calanoid copepod abundance than equivalent sized non-feeding larvae.

DISCUSSION

In general, the principal prey taxa of larval delta smelt have probably changed very little since the latter 1970s. Moyle et al. (1992) presented the only historical diet data for larval delta smelt. Their results were based on a sample of only 24 larvae collected in 1977. This small sample had a diet that was 100% copepods, 99% of which was *E. affinis* and cyclopidae. Given much larger sample sizes, I found other copepods and

Table 4. Results of a Separate Slopes Analysis of Covariance testing for ontogenetic and environmental influences on feeding incidence of larval delta smelt. Feeding incidence was defined as the presence or absence of food in the gut (Dauvin and Dodson 1990). The explanatory variables included in the analysis were larval standard length (SL) as a categorical variable in bins of approximately equal sample size (n = 204-205 fish/bin) and the interaction of SL with two continuous variables; principal components scores (PC1 and PC2) summarizing physical and biological variables taken concurrently with each larva. PC1 primarily represented a gradient in calanoid copepod abundance. PC2 represented a gradient in water clarity (Secchi disk depth) that separated a wet year (1993) from two dry years (1992 and 1994).

Explanatory variable	df	Wald statistic	*P*-value
SL bin	4	69.36	< 0.000001
SL bin X PC1	5	55.68	< 0.000001
SL bin X PC2	5	5.767	0.33

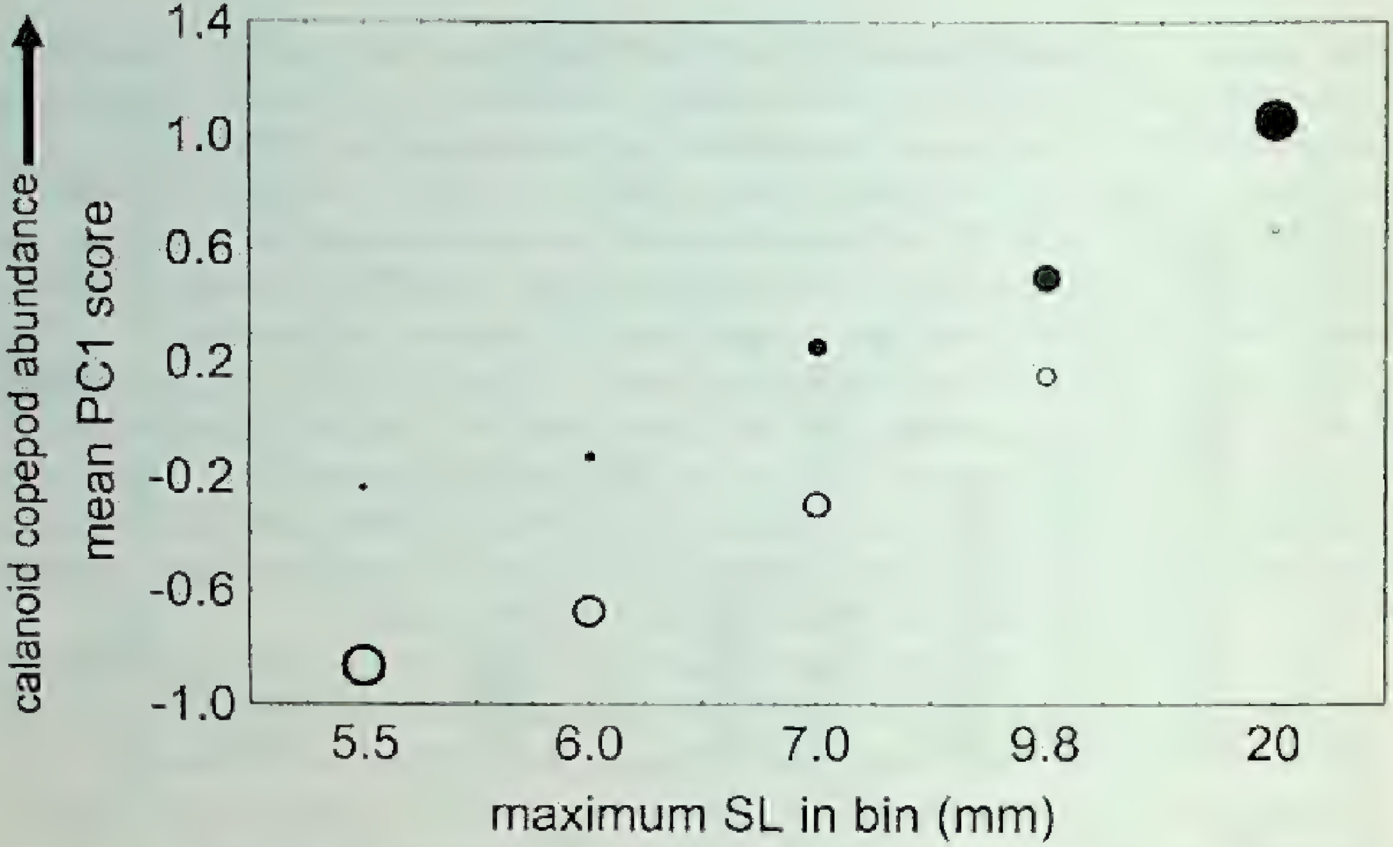

Figure 4. Interactive influences of larval delta smelt standard length (mm) and calanoid copepod abundance on larval delta smelt feeding incidence (FI; the proportion of larvae with food in their gut). The larvae collected with food in their gut are represented by solid circles and larvae collected with empty guts are represented by open circles. The calanoid copepod abundance values are scores from the first principal component of a Principal Components Analysis of physical and biological data collected concurrently with each larval delta smelt. Four copepod abundance variables (nauplii, calanoid copepodites, adult *Eurytemora affinis*, and adult *Pseudodiaptomus forbesi*) loaded strongly (loading of each > 0.80) onto PC1, with abundance of each increasing in a positive direction. Each SL bin on the x-axis represents 204-205 fish and the size of the datapoints represents the proportion of fish in each SL bin with and without food in their guts.

non-copepod zooplankton are occasionally eaten as well. However, despite higher diet diversity than previously reported, both the diet composition (Table 2) and electivity results (Fig. 2) suggest larval delta smelt remain heavily dependent on *E. affinis* and cyclopids as prey. Because both *E. affinis* (Kimmerer and Orsi 1996) and cyclopids (Obrebski et al.[4] 1992) have declined in abundance since the 1970s, it follows that prey abundance for larval delta smelt has declined.

P. forbesi, introduced in 1987 (Orsi and Walter 1991), was important in the diet in 1992 and in June of the other years (Table 2). *P. forbesi* abundance increases in late spring (Kimmerer and Orsi 1996). Meng and Orsi (1991) concluded *P. forbesi* bloom timing would result in temporal mismatch with the emergence of striped bass larvae in the San Francisco Estuary. The low delta smelt FI in 1992 (Fig. 3) and the typically low

[4]Obrebski, S., J.J. Orsi, and W.J. Kimmerer. 1992. Long-term trends in zooplankton distribution and abundance in the Sacramento-San Joaquin Estuary. Interagency Ecological Studies Program for the Sacramento-San Joaquin Estuary Technical Report 32.

occurrence of *P. forbesi* in the delta smelt diet until early summer (Table 2), are evidence that *P. forbesi* also is of limited use to delta smelt larvae even though it is the predominant prey for older delta smelt collected in summer and fall (Moyle et al. 1992; Lott[5] 1998).

The Vanderploeg-Scavia electivity index is awkward to interpret because it is asymmetrical around its random feeding value of zero (Lechowicz 1982). The minimum value of the index is always -1, but the maximum value increases depending on how many prey are considered for analysis. Since I used six prey categories, the maximum index value possible was 0.7. This asymmetry was the likely reason mean electivity was negative for most prey types (Fig. 2). Despite this limitation, Lechowicz (1982) recommended the Vanderploeg-Scavia index because, unlike many other commonly used electivity indices, it was stable under changes in relative abundance of prey types.

Because the smallest delta smelt larvae had usually eaten copepod nauplii and other small prey (Fig. 1) that were not sampled quantitatively by the CB net, the electivity analysis also under represented the prey selection of the smallest larvae with the lowest FI. However, the analysis was sufficient to demonstrate that larval delta smelt capture a subset of the potentially available zooplankton with which they co-occur. Clearly, *S. doerri* and cladocera were rare in the diet for reasons other than low abundance (Table 1; Fig. 2). A study of native and introduced copepods of the San Francisco Estuary demonstrated *S. doerri* has a well developed escape response that made it difficult for larval striped bass to capture (Meng and Orsi 1991). Presumably, the lack of an electivity response to *S. doerri* indicates it is also difficult for larval delta smelt to capture. Larval delta smelt also showed no electivity response to cladocera, which are commonly used in larval fish feeding experiments (Bremigan and Stein 1994; 1997) and are therefore probably not difficult to capture. Cladocera were eaten in low numbers throughout the larval period, indicating size biased predation was also not the reason for lack of use.

As in many larval fishes (Siefert 1972; Hunter 1981), prey size increased as the delta smelt grew. Ontogenetic diet shifts are important for maximizing energy intake during a period of rapid growth (Tsai 1991) and are generally made possible by morphological development resulting in increased mouth gape, fin ray development, and air bladder inflation. Delta smelt mouth width increased continuously throughout the larval period, allowing for ingestion of larger prey. Delta smelt develop fin rays at about 13 mm total length (Wang[2] 1991). It is possible the final diet shift to adult copepods, which occurs at a similar size (Fig. 1), is facilitated by fin ray development.

The analyses of FI also provided important insights into larval delta smelt feeding ecology (discussed below). FI was a coarse, but appropriate metric of feeding success. Because 50% of the larvae examined did not have food in their gut, FI encompassed much of the variability in larval delta smelt feeding success. Although it is likely some larvae evacuated their gut contents upon capture, the larvae were collected using the same techniques and protocols each year. Furthermore, 1994 FI > 1993 FI > 1992 FI was

[5]Lott, J. 1998. Feeding habits of juvenile and adult delta smelt from the Sacramento-San Joaquin river estuary. IEP Newsletter (Interagency Ecological Program for the San Francisco Estuary) 11(1):14-19.

true throughout the larval period (Fig. 3), which is a non-random pattern.

The interannual variability in feeding success at size (Fig. 3), suggests larval food supply may be limiting in some years. Moyle et al. (1992) hypothesized larval delta smelt feeding success would be enhanced in years of high freshwater flow into the estuary because the flows would facilitate seaward movement toward, and subsequent retention in, the LSZ where copepod abundance maxima historically occurred. However, feeding success did not appear to be enhanced in the wet year relative to the dry years (Fig. 3). Following the introduction of *P. amurensis*, copepod abundance maxima shifted up-estuary into less saline water (Kimmerer and Orsi 1996), possibly altering a historical benefit of the LSZ for larval delta smelt. In addition, the abundance of copepods commonly eaten by larval delta smelt does not appear to be related to freshwater flow into the estuary during spring (Jassby et al. 1995; Kimmerer and Orsi 1996). Therefore, the available evidence suggests prey abundance does not consistently differ among years of higher and lower spring outflow.

Larval delta smelt feeding success was influenced by interactions of ontogenetic and environmental influences. If the entire larval period is considered, ontogeny (size of the fish) exerted the largest influence on feeding success (Fig. 3). This is consistent with studies of other larval fishes, which have demonstrated feeding success typically increases with size and experience (Hunter 1981; Gerking 1994). However, differences in FI among years indicate environmental influences were important, particularly once exogenous feeding was fully initiated (Fig. 3). It appears that larval delta smelt feeding success was related directly to prey abundance because (1) the PC1 represented a calanoid copepod abundance gradient, and (2) PC1 scores of feeding larvae were consistently higher than PC1 scores of equivalent sized nonfeeding larvae (Fig. 4). Although a link between food abundance and feeding success is intuitive, it has not been previously demonstrated for any larval fish in the San Francisco Estuary, and it suggests long-term declines in copepod abundance have likely impacted larval delta smelt feeding success.

Overall, the findings of this study are consistent with the hypothesis that long-term declines in copepod abundance and changes in copepod species composition have had a negative impact on delta smelt. Although evidence for starvation due to food limitation is rare in larval fishes, reductions in prey availability can affect larval fish survival indirectly by reducing growth rates (Houde 1987). Reduced growth rate increases the duration of the larval stage, which can result in lower survival through the larval stage. Determining whether or not there is a link between larval feeding success, larval growth rates, and survival is an obvious next step. This research is currently underway (William Bennett[6], personal communication). Clearly, a fuller understanding of direct and indirect effects of food web alteration on delta smelt recruitment is needed for effective management toward recovery.

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[6]Bodega Marine Laboratory, 2099 Westside Rd., P.O. Box 247, Bodega Bay, CA 94923, personal communication via electronic mail on October 18, 2002.

ACKNOWLEDGMENTS

This study was part of the Interagency Ecological Program (IEP), a cooperative San Francisco Estuary research effort. I thank R. Brown, Z. Hymanson, and T. Sommer (CDWR) and P. Herrgesell, D. Sweetnam, and J. Lott (CDFG), who facilitated IEP support. I gratefully acknowledge L. Lynch and the CDFG Central Valley Bay-Delta Branch staff for laboratory assistance. Lastly, I thank my California State University Sacramento Master's Thesis Committee (C. D. Vanicek, J. Lott, P. Roe, and M. Baad) for their helpful guidance during my initial attempts to analyze these data, and L. Brown and W. Kimmerer for their review and helpful comments, which improved the manuscript.

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Received: January 7, 2002
Accepted: November 1, 2002

California Fish and Game 88(4):165-177 2002

SAMPLING METHODS AND TRAPPING SUCCESS TRENDS FOR THE MOHAVE GROUND SQUIRREL, *SPERMOPHILUS MOHAVENSIS*

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The Mohave ground squirrel, *Spermophilus mohavensis*, is listed as threatened by the California Fish and Game Commission. Challenges to this listing have focused on the general lack of information on this species, which prompted this review of sampling data. We found that current datasets, while a rich source of data on squirrel occurrences, are of limited use for developing Mohave ground squirrel habitat models because survey methods varied in reliability, surveys that did not find squirrels are rarely reported, and many important environmental variables were inconsistently reported. To improve the utility of future datasets, we recommend that reports attempt to include 40 variables related to trap characteristics, trapping protocol, demographic features, health information, weather parameters, and site descriptions. We also found that trapping success decreased significantly between 1980 and 2000 across most of the Mohave ground squirrel range, and this decline was not correlated with winter rainfall which generally increased between 1984 and 1998. We recommend that the results of project surveys and trapping studies should be maintained by the CDFG, allowing for future population trend analyses and development of habitat models. We also recommend that studies be initiated to determine if the decline in trapping success continues into the near future and to identify the causes of this trend.

INTRODUCTION

The Mohave ground squirrel, *Spermophilus mohavensis*, is endemic to approximately 2.0 million ha in the western Mojave Desert (Gustafson 1993[1]), constituting the smallest geographic range of the seven *Spermophilus* ground squirrels in California (based on maps in Hall 1981). The California Fish and Game Commission designated this species as "rare" in 1971 under authority of the State Endangered Species Act of 1970, and

[1] Gustafson, J. R. 1993. Report to the Fish and Game Commission: a status review of the Mohave ground squirrel (*Spermophilus mohavensis*) California Department of Fish and Game, Sacramento, California, USA.

reclassified it as "threatened" in 1985 as stipulated by the California Endangered Species Act of 1984. These designations resulted from concerns that it could become threatened with extinction if special protections were not established.

In 1991, the California Fish and Game Commission received a petition from the Kern County Department of Planning and Development Services requesting that the Mohave ground squirrel be delisted (Gustafson 1993), based in part upon the general lack of information on this species, especially its habitat requirements (SWCA 1993[2]). Most data on the Mohave ground squirrel, especially trapping data, remain relatively inaccessible in unpublished databases and reports. These unpublished data are a potentially important source of information that have not been systematically analyzed.

Because there have been no published reviews on Mohave ground squirrel studies, we feel land managers and scientists dealing with this species would benefit from a synthesis of past study methodologies and results. In this paper we 1) summarize existing data sources, focusing on sampling and reporting methodologies; 2) evaluate the utility of current datasets for developing habitat models and propose new reporting protocols that would facilitate future modeling efforts; and 3) analyze past trends in trapping success. Current data on the Mojave ground squirrel came from two sources: the California Natural Diversity Database and trapping studies. Trapping studies included both land development project surveys mandated by the California Department of Fish and Game (CDFG), and a limited number of independent biological studies. We reviewed each source of data, focusing on study methodologies, results, and utility of using the data for habitat modeling.

EXISTING SOURCES OF DATA

California Natural Diversity Database

The California Natural Diversity Database (CNDDB) is a statewide inventory of the locations and condition of California's rare and endangered plants, animals, and vegetation communities (Bittman 2001). It is a positive-sighting database, meaning that only sites were a species occurs are recorded, but not locations were a species was searched for and not found. Entries into the database are submitted to the CDFG from diverse sources, such as state and federal land management agencies, private conservation organizations, and CDFG-mandated project surveys.

The CNDDB records for the Mohave ground squirrel as of 13 February 2001 consisted of 1,353 individual detections at 264 sites between 1886 and 2000. Detection methods varied, depending on whether animals were in hand and could be closely examined or were observed from a distance. Most of these detections were of individuals that could be examined closely after collection by trapping (72%), roadkill (0.8%), or shooting (0.3%) (Fig. 1a). Other less reliable detections occurred by visual (10%), auditory (0.1%), or unreported methods (16.9%).

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[2] SWCA, Incorporated. 1993. Status evaluation of the Mohave ground squirrel. SWCA, Incorporated, Flagstaff, Arizona, USA.

Although most individuals were detected by trapping (Fig. 1a), most sites with Mohave ground squirrels present were identified using less reliable methods such as visual, auditory, or unreported methods (55%; Fig. 1b). Only 45% of Mohave ground squirrel sites were identified using highly reliable methods (e.g., trapping, roadkill, or shooting) alone or with other methods. Sites with the most detections were those where intensive trapping studies produced multiple detections per sampling period distributed over two or more periods. In addition, 49% of Mohave ground squirrel sites were identified from single detections.

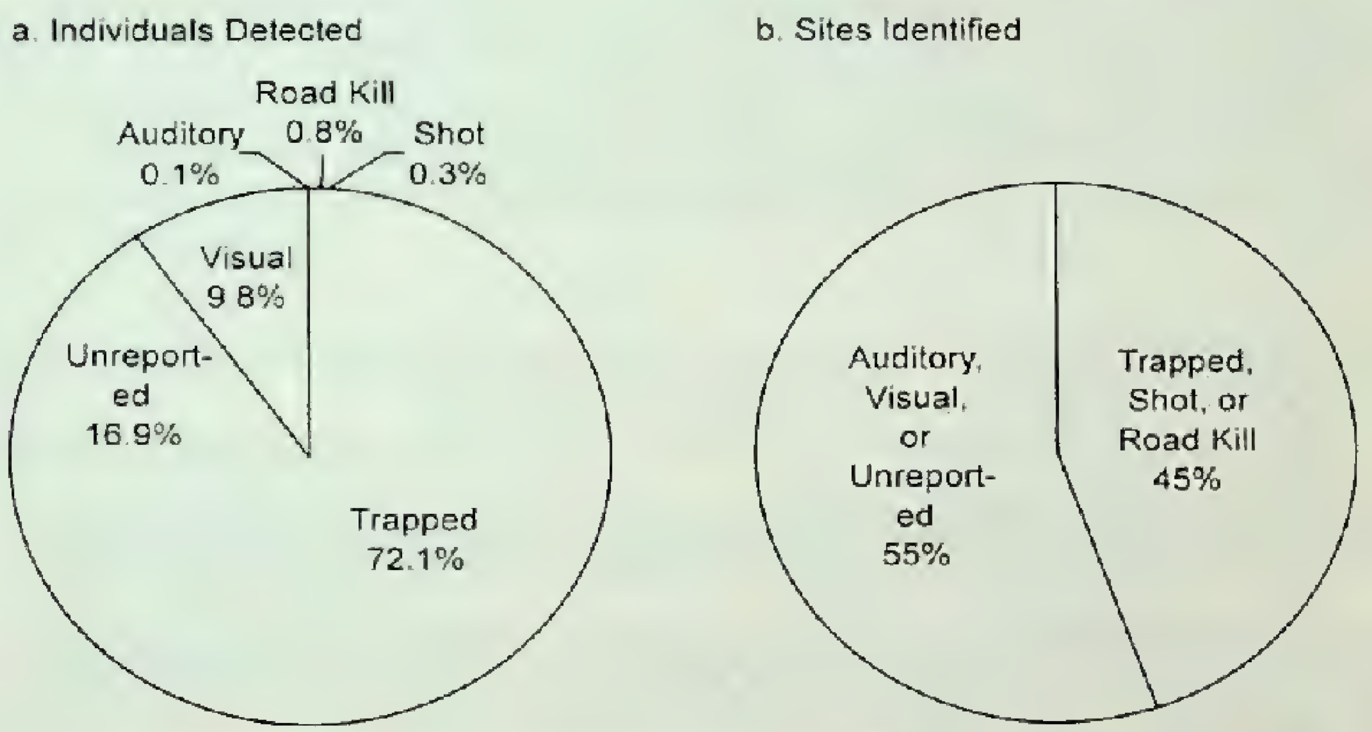

Fig. 1. Methods used to detect individual Mohave ground squirrels (a) and identify sites occupied by Mohave ground squirrels (b), from records between 1886 and 2000 in the California Natural Diversity Database.

Trapping Studies

The Mohave ground squirrel has statutory protection as a threatened species in California. Legislation requires the CDFG to ensure that land conversion actions do not adversely affect the species within its historical range. Such actions include residential and commercial development and the construction and maintenance of highways and utility infrastructure. Surveys are required to determine the presence or absence of Mohave ground squirrels on affected sites and mitigation is required if individuals are detected. Standard guidelines specify that a visual survey be conducted initially and, if no squirrels are detected, that a 5-day trapping survey be conducted between 21 March and 31 May, using a standard 4 × 25 grid of Sherman live traps (23 cm long) spaced 25 m apart (more details on the survey protocol are available from the CDFG). The CDFG requires any person conducting these surveys to obtain a Memorandum of

Understanding (MOU) authorizing the work. As conditions of the MOU, surveyors must submit a description of the project site to the CNDDB and report information about capture results when Mohave ground squirrels are found. Surveyors are not required to report variables such as habitat quality or demographic data.

We summarized the variables reported in 19 Mohave ground squirrel trapping studies (Grinnell and Dixon 1918[3], Hoyt 1972[4], Recht 1977[5], Wessman 1977[6], Zembal et al. 1979[7], Leitner 1980[8], Aardahl and Roush 1985[9], ERT 1987[10], Michael Brandman Associates 1988[11], ERC Environmental and Energy Services Co. 1989[12], Laabs and

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[11] Michael Brandman Associates, Incorporated. 1988. Phase one: China Lake Naval Weapons Center Mohave ground squirrel survey and management plan. Michael Brandman Associates, Incorporated, Santa Ana, California, USA.

[12] ERC Environmental and Energy Services Company. 1989. Biological survey report of the Gravity Wave Observatory Site, Edwards Air Force Base. ERC, San Diego, California, USA.

Allaback 1991[13], Rempel and Clark 1991[14], Recht 1994[15], Recht 1995a[16], Recht 1995b[17], Scarry et al. 1996[18], Leitner 1998[19], Leitner and Leitner 1998[20], Leitner 2001[21]). These reports were identified after an extensive survey of land managers, researchers, and environmental consultants familiar with the Mohave ground squirrel. Most of these studies were project surveys required by the CDFG, while a few were independent biological studies. Only two of these studies were published in widely available scientific periodicals: Grinnell and Dixon (1918) and the Zembal et al. (1979) report summarized in Zembal and Gall (1980). The other 17 studies were described in unpublished reports that were difficult to identify and obtain because they did not show up in standard literature searches.

We identified 40 variables that are important to consider when synthesizing the results of Mohave ground squirrel trapping studies. These variables relate to trap characteristics, trapping protocols, demographic information, health information, weather parameters, and site descriptions. The reporting frequencies varied widely among these variables, and 20% were not reported in any of the 19 trapping studies we analyzed (Table 1).

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[13] Laabs, D., and M. Allaback. 1991. Mohave ground squirrel study, El Mirage Cooperative Management Area, San Bernardino County, California. Biosearch Wildlife Surveys, Santa Cruz, California, USA.

[14] Rempel, R. D., and D. J. Clark. 1991. 1990 Indian Wells Valley Mohave ground squirrel survey, interim report. California Department of Fish and Game, Fresno, California, USA.

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[20] Leitner, P., and B. M. Leitner. 1998. Coso grazing exclosure monitoring study: Mohave ground squirrel study, Coso Known Geothermal Resource Area, major findings, 1988-1996, final report. Phillip Leitner, Orinda, California, USA.

[21] Leitner, P. 2001. California Energy Commission and Desert Tortoise Preserve Committee, Mohave ground squirrel study, final report for 1998-1999. Phillip Leitner, Orinda, California, USA.

Table 1. Important variables to consider when synthesizing results of Mohave ground squirrel trapping studies, and their frequency of reporting among the 19 studies analyzed.

	Count	%[a]		Count	%
Trap characteristics			Demographic information		
Type	19	100	Sex	15	79
Cleaning	0	0	Age class	13	68
History of use	0	0	Reproductive status	8	42
Trapping protocol			Body mass	11	58
Shelter	15	79	Health indicators		
Trapping dates	19	100	Pelage condition	0	0
Time opened	15	79	Condition of eyes	0	0
Time closed	15	79	Condition of nose	0	0
Time checked	16	84	Trauma	0	0
Days trapped	17	89	Behavior condition	0	0
Trapping intervals	17	89	Weather parameters		
Bait type	18	95	Temperature	2	11
Bait amount	0	0	Wind	1	5
Pre-baiting	6	32	Cloud cover	1	5
Years trapped	17	89	Rainfall	1	5
Time caught	6	32	Site description		
Array dimensions	18	95	Location	13	68
Array number	18	95	Topography	7	37
Trap spacing	17	89	Elevation	10	53
Traps per array	17	89	Slope/aspect	6	32
			Soil type	9	47
			Vegetation cover	7	35
			Vegetation species	9	47
			Land-use history	4	21

[a]percentage of 19 trapping studies

Many of these variables are easy to quantify and should be included in future reports to facilitate efforts to synthesize the results of multiple trapping studies. For example, potentially important information on the animal species previously collected in the traps and on the history of trap cleaning was never reported. Mammals rely strongly on olfactory communication (Vaughan 1986) and individuals may leave pheromones in urine and feces voided while inside traps. This could possibly affect the behavior of others subsequently approaching the traps. Extensive descriptions of trapping protocol were included in most reports. However, the times of day at which animals were caught and the amount of bait used were, respectively, rarely or never reported. Demographic information, which was reported for most studies, should be included in all reports, considering the ease with which it can be recorded and its importance in population viability analyses. Indicators of general health were not reported for any of the past studies, but basic health variables should be noted in the future because disease may be a significant threat to uncommon species with limited

ranges. Weather conditions were not documented for most of the studies, even though animal activity levels and the frequency of trap encounters may vary widely due to weather. Site descriptions were lacking in several categories, most notably physical characteristics of the landscape, soils, and vegetation. Although human impact is a primary reason for this species being protected, only 21% of the reports described land-use history at trapping sites.

Most trapping studies were conducted for only 1 year (Fig. 2a), which provides relatively little information for a small mammal species that can fluctuate greatly in numbers among years. Multi-year studies spanning periods of contrasting rainfall are needed for many reasons, not the least of which is to identify possible core areas or refuge habitats where populations may persist during drought years. Most trapping

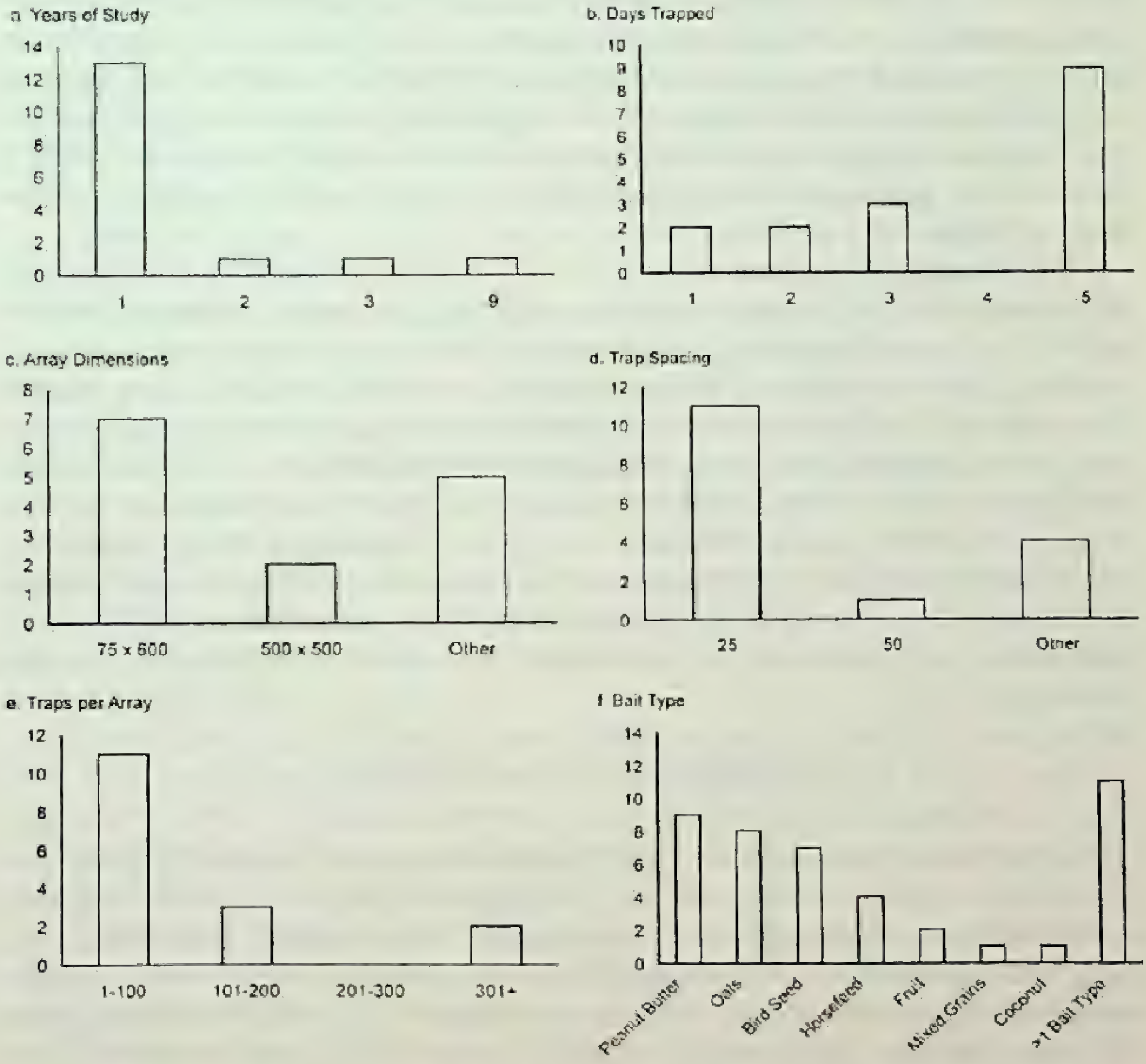

Fig. 2. Reporting frequency of selected trapping variables among 19 Mohave ground squirrel trapping studies. Sample size varied among variables and was always <19 because none of the variables were reported in all of the studies.

was done for multiple days (Fig. 2b), which is appropriate protocol for small mammal studies (Thompson et al. 1998). Trapping array dimensions varied considerably among these studies (Fig. 2c), although the trap spacing (Fig. 2d) and the number of traps per array (Fig. 2e) were relatively consistent. The types of bait used also varied widely (Fig. 2f), and in many cases baits were a mixture of many types.

DEVELOPING HABITAT MODELS

The CNDDB is a rich source of occurrence data for the Mohave ground squirrel. Reported occurrences are spatially referenced within the database, so sites could be readily cross-referenced with other spatially-explicit environmental databases, such as vegetation, soils, topography, and climate. Moreover, site records, especially more recent ones, do list various environmental attributes associated with the site, which would facilitate habitat modeling. However, because the CNDDB is only a positive-sighting database, valid habitat modeling could not be accomplished by using this data alone. Because areas where squirrels were searched for but not found are not recorded in the database, a CNDDB-based habitat model could not conclusively rule out the environmental ranges where the squirrel does not occur. Supplementing the CNDDB database with past or present trapping studies that document no squirrels could be used to overcome this problem.

Trapping studies are also an important data source for habitat modeling, but inconsistent reporting makes valid modeling difficult. Ecological characteristics of the sites were either unreported or were incompletely or inconsistently reported, and all were of unknown accuracy. These sites could be revisited to collect more detailed environmental data, but inconsistent precision in reporting site locations and potential changes in habitat and Mohave ground squirrel populations since the original study limit the feasibility and validity of this approach. Other limitations include non-random selection of survey sites (which are biased toward roads and project locations), infrequent documentation of sites where individuals were not found, and frequent absence of information on life history characteristics and population densities at the detection sites. Future surveys must be more thorough if the data is to be used for habitat modeling.

TRAPPING SUCCESS TRENDS

While presently available data cannot readily be used for habitat modeling, changes in trapping success over time can be used to infer general population trends. Trapping success rates were calculated as the number of individuals captured per 100 trap-days using data reported in the 19 trapping studies mentioned previously. These studies contained trapping data from multiple sites and years. Some studies had several sites within close proximity of each other (1-2 miles). During some years these clustered sites comprised the majority of sites sampled, resulting in a regional bias in the sampling intensity for that year. To minimize this bias, we combined these clustered sites prior

to analyses. This pooling condensed 220 raw data points (sites within year) into 178. Most of the pooled data came from three studies: 31 trapping sites combined into 4 sampling points for data reported in Rempel and Clark (1991), 22 sites into 18 points in data from Aardahl and Rousch (1985), and 15 sites into 8 points from data in Zembal et al. (1979). Three other studies (Wessman 1977, ERT 1987, and Labs and Allaback 1991) had between one and two sites combined each. We performed analyses on both pooled and unpooled data and found no differences in the statistical significance of the results, so we only report statistics from the pooled data. Some studies also reported data from multiple trapping intervals at each site within a given year, which we averaged over the intervals to generate a single data point for that year. Trends in trapping success were evaluated using Spearman rank-order (r_s) correlations, and correlations were only reported if $P \leq 0.05$. We did not attempt to apply parametric statistical models because trapping success data were strongly skewed toward zero values and not normally distributed (Shapiro-Wilk test, $W = 0.71$, $P < 0.0001$).

A total of 178 trapping success values was generated for individual sites during separate years between 1972 and 2000. Samples were clustered in the Coso geothermal region in the northwest part of the range ($n = 54$), and the rest were spread out mostly south of Inyo County, California ($n = 124$; Fig. 3). Overall trapping success averaged 0.82 individuals/100 trap-days, but 35% of the values were 0 and only 13% were >2.

Trends in trapping success differed between sites in the Coso region and sites scattered throughout the rest of the range. At Coso, overall trapping success was 1.15 ± 1.30 SD individuals/100 trap-days. The averages were similar in 1978-1979 (1.50 ± 1.44) and 1987-2000 (1.01 ± 1.23), and trapping success was not significantly correlated with year (Fig. 4). At the non-Coso sites, trapping success averaged 0.67 individuals/100 trap-days, but the rates of success differed between 1972-1977 (0.42 ± 0.89), 1980 (2.04 ± 1.84), and 1987-2000 (0.46 ± 0.72). Although the overall correlation between trapping success and year at non-Coso sites was not significant, success was correlated with year when the 19 sampling sites that were located outside of the Mohave ground squirrel range (Fig. 3) were excluded from analysis ($r_s = -0.25$, $n = 105$). These 19 sites were sampled in 1977 in an attempt to delineate the southeastern boundary of the species range (Wessman 1977), so it is not surprising that Mohave ground squirrels were not found at any of them.

There was an especially strong decline in trapping success from 1980 through 2000 ($r_s = -0.60$, $n = 75$) at the non-Coso sites. Of the variables listed in Table 1, only trap spacing ($r_s = 0.49$, $n = 29$) and the number of days trapped per trapping period ($r_s = 0.48$, $n = 29$) were also significantly correlated with year. However, these variables were not correlated directly with trapping success, and there is no apparent reason why increased trap spacing or number of days trapped should cause a decline in trapping success. Thus, the recent decline in trapping success does not seem to have been associated with systematic changes in the trapping methods that we analyzed.

Fluctuations in rainfall can have significant effects on the abundance of small mammals such as the Mohave ground squirrel (Gustafson 1993), and trapping success was positively correlated with winter rainfall (October-March) from the current ($r_s = 0.38$, $n = 178$) and previous ($r_s = 0.29$, $n = 178$) year. However, multi-year trends between

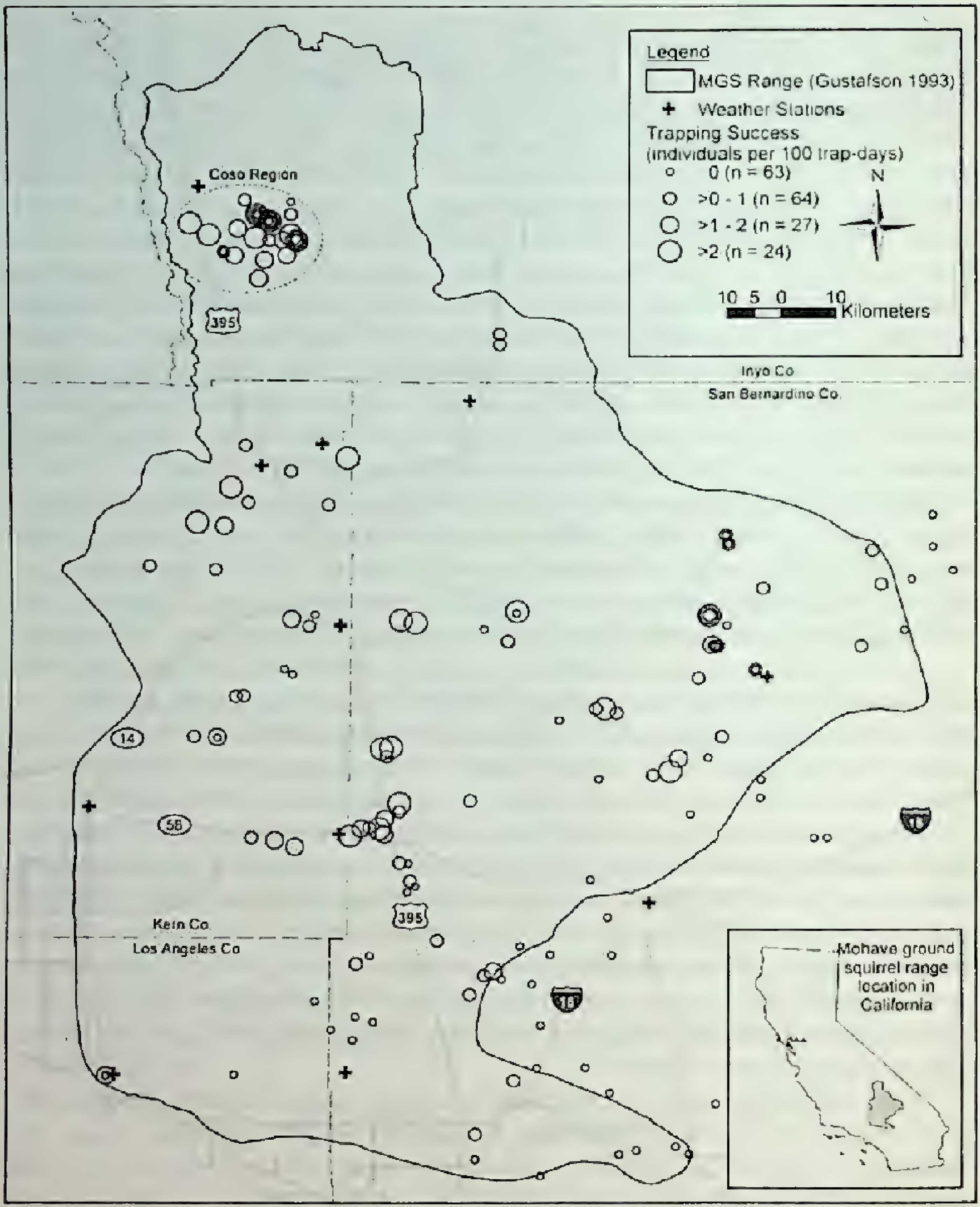

Fig. 3. Locations for 178 trapping success measurements calculated from 19 trapping studies and the 11 NOAA weather stations reported in Fig. 4.

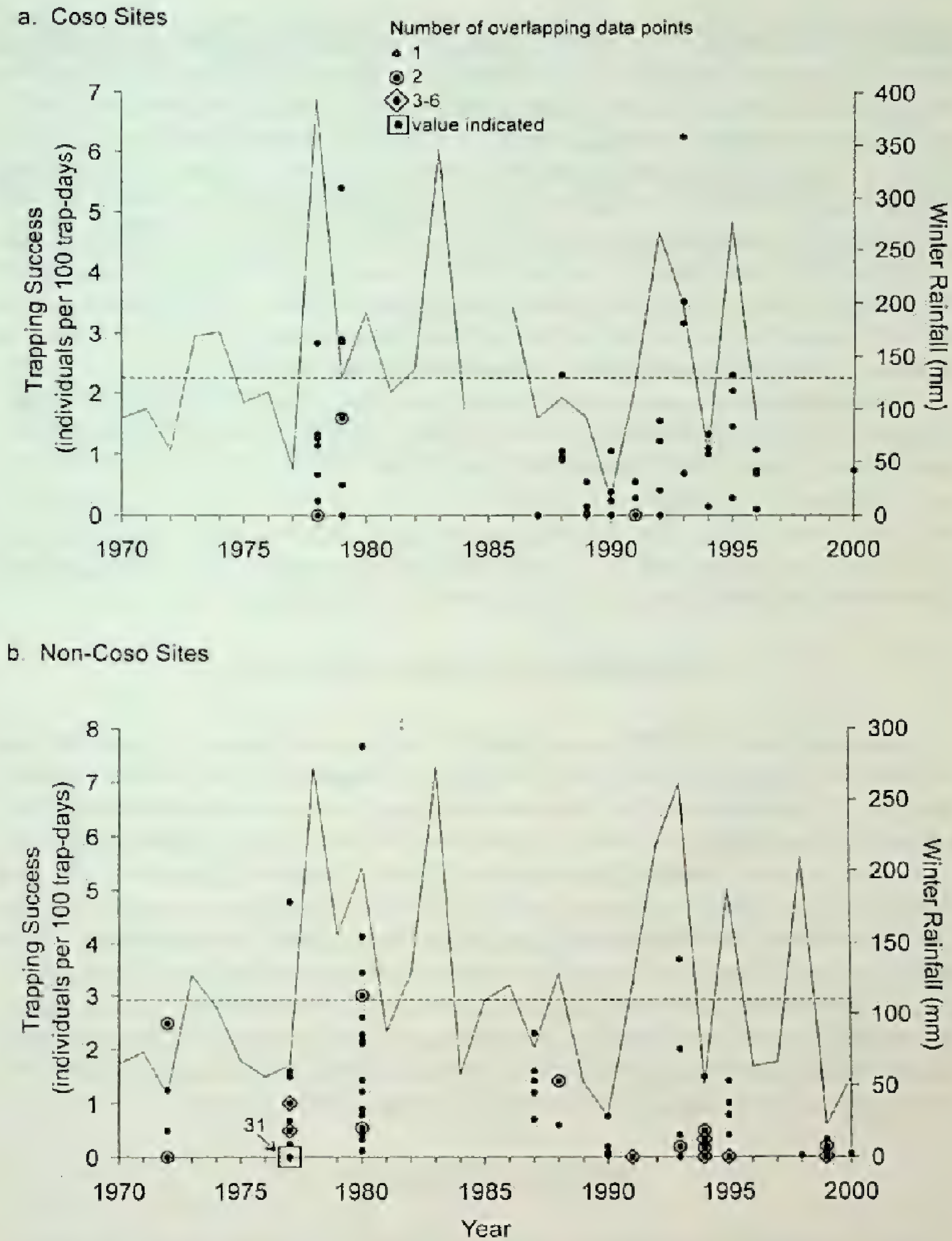

Fig. 4. Trapping success (scatter plot) and total winter rainfall from October through March (line plot) between 1970 and 2000 for the Coso region (a) and sites located in rest of the Mohave ground squirrel range (b). Winter rainfall estimated using data from 1 NOAA weather station for Coso data (Haiwee, 1985 data missing) and 10 additional stations for non-Coso data (Barstow, Boron, China Lake NAF, El Mirage, Goldstone Echo No 2, Inyokern, Mojave, Palmdale, Randsburg, and Trona; http://www.ncdc.noaa.gov). Long-term average winter rainfall is identified on each graph as a horizontal dashed line.

trapping success and winter rainfall varied between the first and last decades of our data set. The period from 1970-1977 had particularly low rainfall, and 1978 marked the end of a 36-year period of relatively low rainfall in the Mojave Desert (Hereford 2000[22]), so is it not surprising that trapping success in 1972 and 1977 was relatively low. Similarly, it is not surprising that increased rainfall beginning in 1978 was followed by increased trapping success during 1980, and decreased rainfall beginning from 1984-1991 was followed by decreased trapping success in 1987, 1988, 1990, and 1991. However, the cycle back from low rainfall in the mid-1980's to high rainfall in the 1990's was not followed by increased trapping success as would be expected. Thus, trapping success has declined across most of the Mohave ground squirrel range since the mid-1980's, and this decline was not associated with decreased rainfall.

Recent attempts to locate populations for new studies have been hampered by low trapping success, even during a period in which winter rainfall was adequate for reproduction and survival (Leitner 2001) and at sites where Mohave ground squirrels were previously abundant from the mid-1970's through the early-1980's. The results of others (Leitner 2001), coupled with the decreased trapping success since the mid-1980's that was summarized here, have heightened concerns that the Mohave ground squirrel may be undergoing a long-term decline in abundance.

MANAGEMENT RECOMMENDATIONS

Reporting to the CNDDB, and to the CDFG for project surveys, should include detailed descriptions of habitat and life history parameters of the Mohave ground squirrels. Trapping studies should include descriptions of trap characteristics, trapping protocol, demographic and health information for the animals captured, weather conditions, and site characteristics listed in Table 1. Results of project surveys and trapping studies should be maintained by CDFG in a database, separate from the CNDDB, for future population trend analyses and development of habitat models. New survey methods should be evaluated to search for study populations and, in the process of searching, generate additional data for a CDFG database. Studies should be initiated to verify that the observed decline in trapping success is due to an actual decline in the abundance of the Mohave ground squirrel, to determine if this trend continues into the future, and to identify the causes of this decline.

ACKNOWLEDGMENTS

This review was supported by an interagency agreement between the United States Geological Survey and the California Department of Fish and Game. K. Berry, T.

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Campbell, J. Gustafson, R. Jones, P. Leitner, and J. Lovich reviewed preliminary drafts that contributed greatly to the final manuscript.

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Received: March 25, 2002
Accepted: December 17, 2002

CALIFORNIA FISH AND GAME
California Fish and Game 88(4):178-180 2002

FIRST RECORD OF THE ARMED GRUNT, *CONODON SERRIFER* (HAEMULIDAE), IN SOUTHERN CALIFORNIA

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On 7 January 1992, an armed grunt, *Conodon serrifer* Jordan and Gilbert, 1882 (Haemulidae), was collected in San Diego County at Southern California Edison Company's San Onofre Nuclear Generating Station (33°22'30" N, 117°33'30" W) during a routine fish monitoring survey. The northern-most collection for this species as referenced in the museum collections of California Academy of Sciences (CAS), the Natural History Museum of Los Angeles County (LACM), and Scripps Institution of Oceanography (SIO) was at Bahia San Juanico, Baja California Sur, Mexico (26°14'N, 112°25'W). Thus, this specimen extends the known range northward approximately 950 km from lower Baja California to northern San Diego County.

The specimen is slightly dusky above and silvery below, with eight black bars extending from the base of the dorsal fin to just below the midline (Fig. 1). When freshly caught, the rayed sections of the dorsal, pectoral, pelvic, anal, and caudal fins had a yellowish color. It measures 154 mm total length (upper lobe of caudal fin missing). 134 mm standard length, and weighs 48 g. Fin element counts are: dorsal (XII + 12), anal

Figure 1. Armed grunt (*Conodon serrifer*) from San Onofre Nuclear Generating Station, San Diego County, California, 134 mm SL; LACM 47322-1. Photo by author.

(III,6), pectoral (15). The dorsal fin is deeply notched, with both sections contiguous. The 2nd anal fin spine is strong, its tip extending almost to the end of the soft rays with the fin depressed. Several teeth in the upper and lower jaws are enlarged and strongly conical. The margin of the preopercle is almost fully serrate with 11 teeth along the ventral margin projecting anteriorly, 8 teeth along the posterior margin projecting dorsally and a single large spine at the angle projecting posteriorly. The length of this spine is approximately one-half the eye diameter. This specimen is deposited at the Natural History Museum of Los Angeles County (LACM 47322-1).

Four other species of grunts are known from California: sargo, *Anisotremus davidsonii*; Cortez grunt, *Haemulon flaviguttatum*; wavyline grunt, *Microlepidotus inornatus*; and salema, *Xenistius californiensis* (Eschmeyer et al. 1983; Lea and Rosenblatt 1992). The body shape of the armed grunt is most similar to that of the wavyline grunt, salema, and Cortez grunt (Table 1). It can be distinguished from them by the presence of multiple bars instead of stripes, the strong spine at the angle of the preopercle, and the large, canine-like teeth on the upper and lower jaws. Additionally, the armed grunt has the fewest anal rays (6-8) of these five species.

It can not be absolutely determined how this individual arrived in California waters. Dumping of live bait collected in southern waters into Los Angeles Harbor by commercial long-range tuna boats was noted as early as 1932 (Clark 1932), however, current long range trips are only conducted by sport-fishing boats which carry their bait with them. Alternatively, fluctuating oceanographic conditions can also bring new species into California waters. Northern range extensions of tropical species have occurred during warm water episodes (Mearns 1988), and during 1991-92 sea surface temperatures were warmer than normal (Lynn et al. 1995). Three additions of southern species to the California fish fauna which also occurred around this time included two species of jacks (bigeye trevally, *Caranx sexfasciatus*, and Mexican lookdown, *Selene brevoorti*, both collected in San Diego Bay (Lea and Walker 1995) and a tripletail, *Lobotes surinamensis*, at San Pedro (Rounds and Feeney 1993).

Table 1. Selected meristic characters of haemulid species known from California.

	Fin Ray Counts				
	Dorsal	Anal	Pectoral	Gill Rakers	Lateral Line
Sargo[1,2]	XI-XII,14-17	III,8-11	17-19	9-12+13-16	54-62
Armed grunt[1,2]	XII,12-13	III,7-8	15-17	7+14	50-55
Cortez grunt[3,4]	X-XII,15-18	III,9-11	16-19	10-11+21	50-53
Wavyline grunt[1,3]	XIII-XIV,15-17	III,12-14	18-21	8+16-17	80
Salema[1,2,3]	IX-XII+I-II,11-14	II-III,9-12	17-19	11-13+15-24	50-55

[1]Watson 1996; [2]McKay and Schneider 1995; [3]Allen and Robertson 1994; [4]Lea and Rosenblatt 1992

ACKNOWLEDGMENTS

The authors thank M. J. Allen (Southern California Coastal Water Research Project) for assistance identifying the species, and both he and R. N. Lea (California Department of Fish and Game) for assistance locating manuscript information. We thank M. J. Allen, R. N. Lea, and R. Rosenblatt for comments on the manuscript. Also, we thank R. F. Feeney (LACM), H.J. Walker (SIO), and D. Catania (CAS) for information from their respective collections. Finally, we thank C. T. Mitchell (MBC *Applied Environmental Sciences*) for his support and review of the manuscript.

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Received: February 5, 1999
Accepted: December 12, 2002

California Fish and Game 88(4):181-185 2002

NEWLY DISCOVERED FOOD AND HABITAT USE BY CALIFORNIA RED TREE VOLES

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The red tree vole, *Arborimus* spp., is an arboreal rodent that inhabits the coastal forests of western Oregon and northwestern California (Zeiner et al. 1990). These forests are located in the humid, temperate region where redwood, *Sequoia sempervirens*, Douglas-fir, *Pseudotsuga menziesii*, western hemlock, *Tsuga heterophylla*, Sitka spruce, *Picea sitchensis*, and western red cedar, *Thuja plicata*, are the dominant tree species. Through karyotype analysis, Johnson and George (1991) determined that the genus is represented by two species: the California red tree vole, *Arborimus pomo*, and the red tree vole, *Arborimus longicaudus*. The California red tree vole occupies the southern portion of the red tree vole's range (Hall 1981), from Bodega Bay north to the Klamath Mountains at approximately the Oregon border (Figure 1).

Red tree voles have a highly specialized feeding behavior. They remove the lateral resin ducts from conifer needles and consume the meduallary portion. The disposed resin ducts accumulate in the arboreal nest, forming the inner lining and base of the nest (Benson and Borell 1931, Hamilton 1962, and Maser 1965). As nests age or are disturbed by weather or animals, clumps of resin ducts fall to the forest floor offering positive evidence of red tree vole activity (Gillesberg and Carey 1991, Meiselman 1992, and Wooster pers. observ.). Red tree voles have been reported to eat the needles of grand fir (*Abies grandis*), white fir (*Abies concolor*), Douglas-fir, western hemlock, Sitka spruce (Benson and Borrell 1931, Ingles 1957, Maser et al. 1981, and Taylor 1915), and the bark and/or cambium from coniferous twigs (Maser 1965 and Nelson 1918).

The California red tree vole was classified by the California Department of Fish and Game as a species of special concern (Williams 1986) because of its affinity for coastal coniferous forests and the potential negative impact of large-scale timber harvests. Due to the restrictive diet of the species, researchers have focused their studies on forests containing fir, hemlock, or Sitka spruce (Aubry et al. 1991, Corn and Bury 1986, Meiselman 1992, and Meiselman and Doyle 1996).

Since 1991, agency biologists, academic researchers, industrial timber company personnel, consulting wildlife biologists, and consulting foresters working in Mendocino and Sonoma counties have surveyed for this vole during the preparation of timber harvest plans. California red tree vole nests are located by searching for stick nest

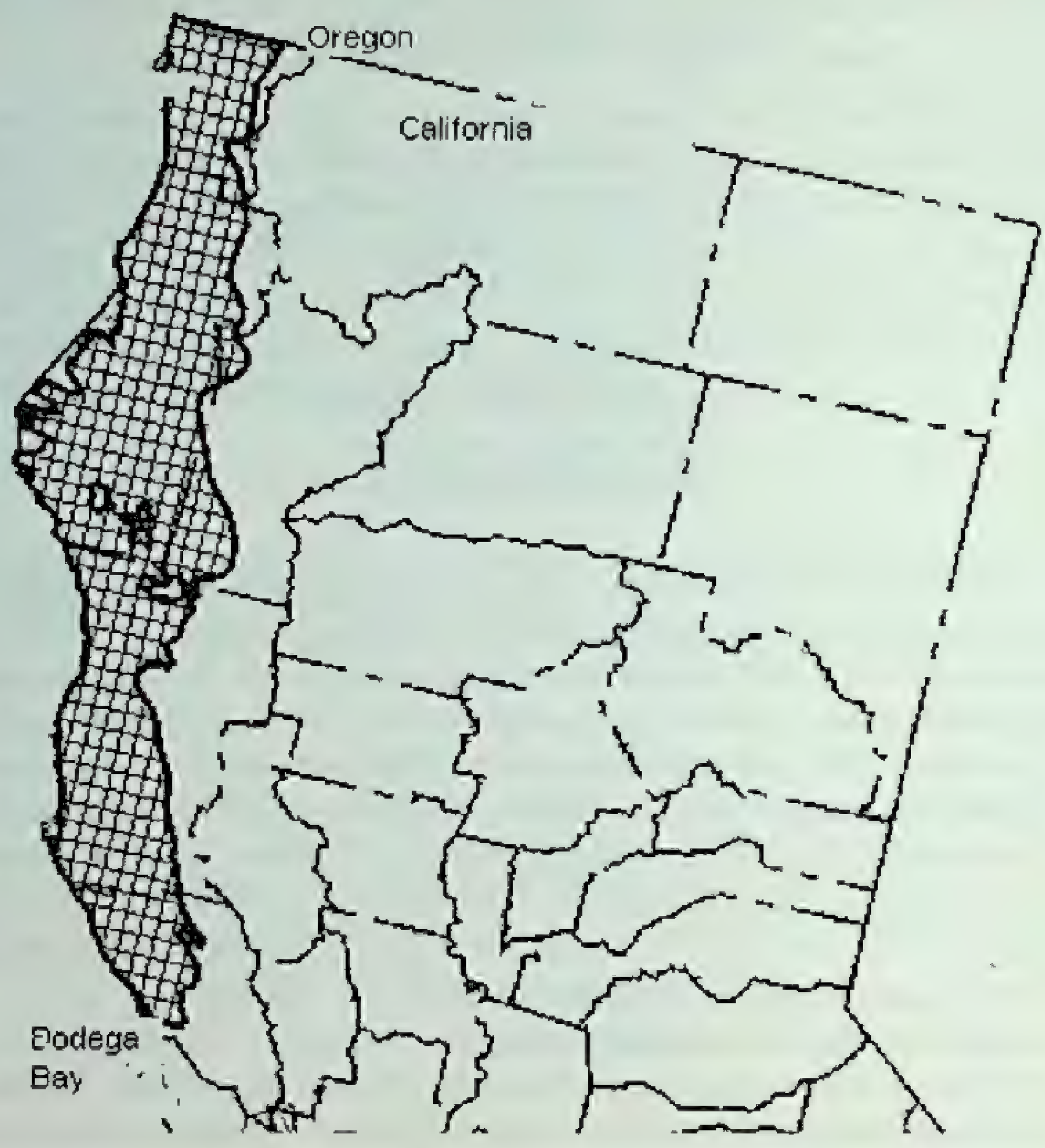

Figure 1. California Red Tree Vole Range.

structures in trees using the unaided eye or binoculars. When a potential nest is located, the surveyor searches the ground below for the presence of resin ducts and nest material. Questionable nests are verified by knowledgeable biologists. Field survey forms are completed on the positively identified nests. Through years of experience searching for red tree vole nests, the authors have found the easiest way to locate potential nests is walking through an area in the winter and early spring. This time of the year, the rains have lowered the conifer branches, deciduous leaves are absent, and wind-storms have blown resin ducts to the forest floor. Nests are usually found along road and riparian edges; however, this may be due to increased visibility to the upper canopy.

Survey efforts led to the discovery of California red tree voles nesting and consuming Bishop pine needles, *Pinus muricata,* in Mendocino County. The first discovery of California red tree voles nesting and feeding in Bishop pine was on 10 September 1994. A 7 by 13-cm wide mass of Bishop pine resin duct remains was found at the base of a Bishop pine in the Moat Creek drainage. The stand was a mixture of

Bishop pine, redwood, and Douglas-fir. On 18 May 1995, a similar mass of material was found in a pure stand of Bishop pine in the Mitchell Creek drainage. On 3 January 1996, the use of Bishop pine was again confirmed when the nest of a California red tree vole was located in a 10-cm dbh Bishop pine in the Jughandle Creek drainage. Inspection of the nest revealed stripped and unstripped Bishop pine and hemlock needles, and their resin ducts. As further confirmation of species identification, a live adult red tree vole was captured in the nest material. The latest location of California red tree voles nesting in Bishop pine was found on 27 July 2001. Beneath a 61-cm dbh Bishop pine was a pile of Bishop pine resin ducts. The stand was a mixture of Bishop pine, redwood, and Douglas-fir.

All four locations (Figure 2) of red tree voles utilizing Bishop pine are close to the coast where there is approximately a 3-km wide band of this tree species. This band extends from below the known southern edge of the red tree voles' range near Freestone to just north of Fort Bragg (Griffin and Critchfield 1972). It is unknown whether California red tree voles are moving into a new habitat or have always occurred there.

Figure 2. Location of California Red Tree Voles Utilizing Bishop Pine

Red tree voles utilizing Bishop pine can be difficult to identify because as the needles drop they form massive layers on the branches and on the ground, making nests and resin ducts difficult to locate.

These records expand the known forage and nesting habitat of the California red tree vole. The confirmation of a nest in a pure Bishop pine stand adds to the vegetation types that the species is known to inhabit.

ACKNOWLEDGMENTS

The authors thank L. Susan for discovering and notifying the authors about the use of Bishop pine by red tree voles. Helpful suggestions for this manuscript were provided by B. Valentine, D. McGriff, and C. Town. Special thanks to all the natural resource professionals who participate in the identification and continued update of the California red tree vole database.

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Received: June 3, 2002
Accepted: November 27, 2002

California Fish and Game 88(4):186-195 2002

TIME ALLOCATION BY ALEUTIAN CANADA GEESE DURING THE NONBREEDING SEASON IN CALIFORNIA

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INTRODUCTION

The proportion of time an animal allocates to various activities during the different periods of the annual cycle help to describe its ecological adaptations. Time-activity budgets constructed for a population may provide information about the response of the population to environmental factors and aid in the management of the population (Paulus 1988).

The Aleutian Canada goose, *Branta canadensis leucoparia*, is one of several subspecies of Canada geese found in the Pacific Flyway along the west coast of North America (Bellrose 1976). After the May to September breeding season, the majority of Aleutian Canada geese in the Aleutian Islands migrate to staging and wintering grounds in northern and central California.

The objectives of this study were to describe habitat use and activity patterns of Aleutian Canada geese during the nonbreeding season in California. Patterns of time allocation by geese between seasons and among locations are discussed relative to diet and nutrient requirements for winter survival, migration, and reproduction.

METHODS

Time-activity budgets of Aleutian Canada geese were studied at their major concentration areas in California from January to March and October to December 1993. Geese staged during the fall in an area near Crescent City (hereafter, northern coast [NC]) and in the Sacramento Valley (SCV) before moving to the terminal wintering area in the San Joaquin Valley (SJV). In the spring, Aleutian Canada geese staged in the NC before departing for the breeding grounds in Alaska.

During this study, Aleutian Canada geese were observed for about 2 weeks at each of their fall migration areas (SCV, 19 to 30 October 1993 and NC, 1 to 13 November 1993).

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8 weeks in their terminal wintering area (SJV, 15 January 1993 to 28 February 1993 and 2 to 18 December 1993), and 3 weeks at their spring migration area (NC, 2 to 25 March 1993).

Sampling began when Aleutian Canada geese left the night roost in the morning and ended upon their return to the roost in the evening. Behavioral observations began when flocks of geese or the observer arrived at feeding or day roosting sites. Observation days were divided into morning (the 3 hr after sunrise), mid-day (from 3 hr after sunrise to 3 hr before sunset), or afternoon (the 3 hr before sunset). Sunrise and sunset times were taken from Gale Research Company (1977) tables for Eureka (NC), Sacramento (SCV), and Stockton (SJV).

Instantaneous sampling of individual geese followed methods described by Altmann (1974). The behavior of an individual goose was assessed every 20 sec at the sound of a metronome (Wiens et al. 1970). The behavior sampling of an individual goose (termed the 'focal observation') ended after a minimum of 20 min of continuous observation. About 200 geese wearing gray neck-collars engraved with unique identifiers were in the Aleutian Canada goose population during this study. Whenever possible, neck-collared Aleutian Canada geese were sampled to allow for positive subspecies identification of the sampled goose; to confirm that the same goose was under observation as it moved through the flock; and because the sex and age of the individual was known. The sex and age of neck-collared geese was determined at the time of banding. Unmarked geese were selected for sampling only when marked geese were not available. Unmarked geese were selected opportunistically, usually based on having a distinguishing characteristic associated with the white cheek patch. This characteristic allowed the observer to ensure that the same goose was under observation during the sampling period.

Daily reconnaissance of the study areas identified the total population size of Aleutian Canada geese present and enabled the observer to choose undisturbed flocks for sampling in habitats the majority (>50%) of the geese in the study area were using at the time of sampling. Open viewing conditions in the agriculture-dominated study areas allowed the observer to monitor diurnal habitat use of the goose population segments in the area. Individual flocks within the habitat were then chosen based on observer accessibility. The flock was scanned with a 20x spotting scope in a zig-zag manner when searching for a neck-collared focal bird to help reduce the bias of searching only certain portions of the flock (e.g., the portion of the flock closest to the observer). All observations throughout the study were made by the senior author mostly from a vehicle or a tent blind. General habitat types (i.e., agricultural field type, harvested vs. unharvested, water body, etc.) were noted for areas used by Aleutian Canada geese during the focal observations.

Behaviors of the geese were grouped into six general activity categories: (1) feeding (head down while stationary or moving; drinking); (2) resting (head under wing or on back); (3) maintenance (preening, bathing, and other comfort behaviors as described by McKinney [1965]); (4) locomotor (walk or swim with head up); (5) alert (stationary with head and neck up); and (6) social (antagonistic; flight initiation head tossing as described by Raveling [1969]). Behavioral data were recorded with tally counters and cassette recorders and later transcribed to data sheets. The proportion of time a particular activity occurred was determined by dividing the number of instantaneous

observations for that particular activity by the total number of all instantaneous observations during the focal observation.

Non-parametric tests were used for analyses because of the heterogeneous variances of the means and non-normal distribution of the data. Within each geographic location or season, Kruskal-Wallis or Mann-Whitney U-tests were used to detect differences among the means of the different activities as dependent variables and daily time period as independent variables (Zar 1984, SPSS Inc. 1990). To test for differences in the time spent in activities among or between locations and seasons, the Kruskal-Wallis test was used to compare means of activities for all observations (Zar 1984, SPSS Inc. 1990). Dunn's multiple comparisons were used to separate significant results of Kruskal-Wallis tests (Zar 1984). Social activity was excluded from statistical analyses because of the low frequency of this behavior and lack of an adequate sample size for analysis. Statistical tests were two-tailed with a significance level of $P < 0.05$.

RESULTS

Sample Observations

A total of 456 focal observations was made of Aleutian Canada geese during the study. Of 429 observations of marked geese, 353 observations (82%) were of adults and 76 observations (18%) were of juveniles or yearlings. The 429 observations of marked geese include repeated observations distributed among 145 unique individuals with a maximum of 12 observations of the same goose. An additional 27 observations were made of unmarked geese or of geese whose bands were not completely identified. The length of focal observations averaged 24 to 39 min among the locations and seasons (Table 1). A 60:40 ratio of male to female marked Aleutian Canada geese were sampled for activities during the study. Study design and sample size limitations precluded an analysis of time allocation by age or sex.

Aleutian Canada geese were often found in mixed flocks with cackling Canada geese, *Branta canadensis minima*. The percent of cackling Canada geese in mixed flocks was highest in the SCV and SJV, ranging from about 10% to 30%. Fewer cackling Canada geese were present in the NC and generally comprised less than 5% of the flocks. Small flocks (< 600 individuals) of snow, *Chen caerulescens*, Ross's, *C. rossii*, greater white-fronted, *Anser albifrons frontalis*, and/or Western Canada geese, *Branta canadensis moffitti*, were sometimes associated with the Aleutian Canada goose flocks at feeding or roosting areas, primarily in the SJV. Flock sizes of Aleutian Canada geese during focal observations were generally between 1,000 and 7,000 geese, except during the fall in the NC, when flock sizes were less than 600 geese. The estimated population of Aleutian Canada geese wintering in California was 11,680 in 1992-93 and 15,700 in 1993-94 (Dahl et al.[2] 1994).

[2]Dahl, A.L., H.C. Stabins, C.E. Grue, and D.A. Manuwal. 1994. Aleutian Canada goose project: migration and wintering areas in California and Oregon. Progress report - Oct. 15, 1993 to Apr. 17, 1994. Unpubl. rpt. Washington Cooperative Fish and Wildlife Research Unit, University of Washington, Seattle, Washington, USA.

Table 1. Proportion of time spent in activities during daylight hours by Aleutian Canada geese during the nonbreeding season and among locations and seasons -- North Coast (NC), Sacramento Valley (SCV), and San Joaquin Valley (SJV), California, during 1993.

	Overall nonbreeding	NC	SCV	SJV	NC
Activity	season	Fall	Fall	Winter	Spring
Feeding	52.9 ± 1.4[a]	62.6 ± 1.7 A[b]	48.0 ± 3.4 AB	42.9 ± 2.0 B	78.8 ± 1.2
Maintenance	14.4 ± 0.8	8.2 ± 1.0 AB	23.4 ± 2.5	17.0 ± 1.3 B	4.4 ± 0.5 A
Alert	14.1 ± 0.6	16.5 ± 1.2 A	13.5 ± 1.2 AB	14.6 ± 1.0 B	10.6 ± 0.8 B
Resting	9.7 ± 0.9	7.5 ± 1.4 A	11.9 ± 2.9 A	11.9 ± 1.4 A	3.1 ± 0.8 A
Locomotor	7.8 ± 0.9	4.9 ± 0.8 A	2.0 ± 0.4	11.7 ± 1.6 A	2.9 ± 0.3 A
Social[c]	0.7 ± 0.1	0.1 ± 0.04	0.9 ± 0.2	1.0 ± 0.1	0.2 ± 0.08
No.[d] =	456	72	64	242	78
Obs. hrs.[e] =	222.6	29.5	30.4	111.9	50.8
Obs. (min)[f] =	29	24	28	29	39

[a]Mean ± SE.
[b]Within an activity, means with the same letters are not different ($P > 0.05$) based on Kruskal-Wallis test or Dunn's multiple comparisons among locations.
[c]Social activity excluded from statistical analyses.
[d]Number of focal observations.
[e]Total hours of focal observations.
[f]Mean time of a focal observation.

Habitat Use and Daily Movements

In all study areas, geese typically flew from night roosts in the morning to feeding sites in pastures or agricultural fields. In the NC during both fall and spring staging periods, geese foraged on dairy and beef cattle pastures with irrigated, fertilized, and selectively seeded graminoid and herbaceous plants. Occasional flights in the SCV and SJV were made during the day from pastures to nearby water bodies where geese drank, bathed, and preened, but geese generally returned to pastures within a half hour. In the NC, the geese generally encountered water bodies without having to fly to them.

In the SCV, geese often flew from the night roost to harvested fields that contained kidney bean, safflower, or black-eyed bean seeds, young sprouts of waste grain, and other herbs and graminoids. After about an hour in these fields, geese moved to

harvested rice fields where they typically stayed for the remainder of the day. Aleutian and cackling Canada geese primarily foraged in rice fields that had been mowed after harvest, which left the stalks and seed heads scattered or in piles on the fields. Aleutian Canada geese were observed pecking and rooting through rice plant debris and pulling lower layers of the debris to the surface. Geese were also observed pecking at the tips of cut rice stalks that were still rooted in the ground. Several of the rice fields were flooded to varying depths (< 15 cm) and geese would forage below the water surface.

In the SJV, Aleutian and cackling Canada goose flocks foraged in both pastures and agricultural fields. Geese departing the night roost would typically congregate on pastures or fields with sprouting cereal grains for usually less than an hour. Geese would then move into corn fields for an intensive feeding period usually lasting 2 to 3 hr. Near mid-day, geese flew in several large groups to roost sites with water. After a period of time in the water loafing and bathing, geese would move out of the water to preen and rest. Geese gradually moved onto surrounding pastures to feed. Some groups would fly back to the water bodies several times during the early afternoon, a pattern especially prominent on warm, sunny days. In the late afternoon, flocks of geese moved to pastures further away from the mid-day roost. About 1.5 to 1 hr before sunset, flocks of geese flew into the corn fields for a second intensive feeding period lasting until near sunset.

Aleutian Canada geese foraged in two types of corn fields in the SJV; harvested corn stubble and unharvested knocked-down corn. Corn stubble fields were harvested before the geese arrived and existed in plowed or unplowed conditions during use by geese. Approximately 20 ha of corn in the study area were not harvested and were made available to geese by knocking the stalks to the ground with a tractor. Portions of the unharvested corn were knocked to the ground when the geese first arrived in the area and additional portions were knocked down throughout the winter.

Daily and Seasonal Time Allocation

Aleutian Canada geese spent most of the daylight hours feeding (Table 1). Maintenance and alert activities were also common activities. In the morning and/or afternoon periods, time spent feeding and alert was greater and resting was less when compared to mid-day ($P < 0.05$; Fig. 1).

Aleutian Canada geese allocated more time to feeding during the spring in the NC than in any other location or season ($P < 0.001$; Table 1). Time allocated to feeding during the winter in the SJV was similar to that during fall in the SCV but was significantly less than during the fall in the NC ($P < 0.001$).

DISCUSSION

Diurnal Activity Patterns

Aleutian Canada geese spent more time feeding and alert in either or both morning and afternoon periods compared to mid-day. This pattern of increased feeding activity in the morning and afternoon has been documented in many waterfowl species (see

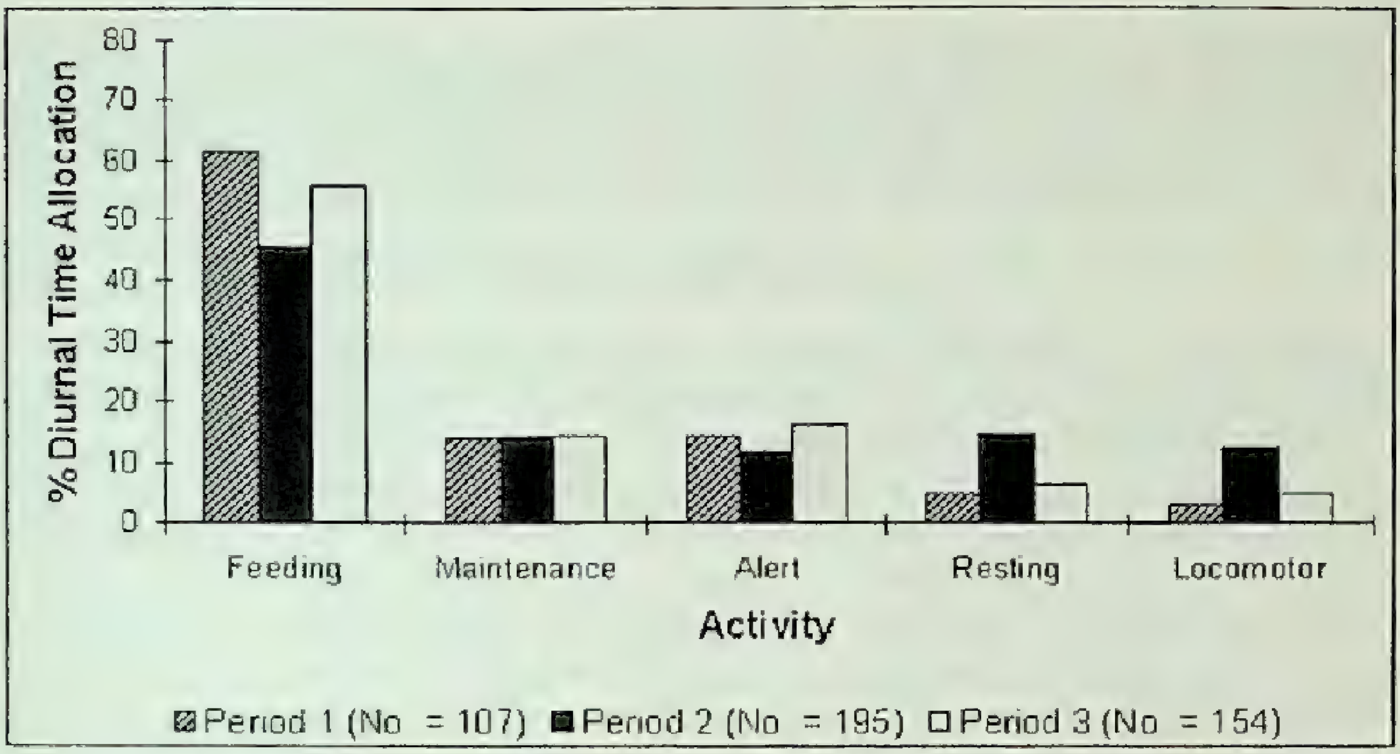

Figure 1. Proportion of time spent in activities by Aleutian Canada geese during the day for the nonbreeding season, California, during 1993. Period 1: from sunrise to 3 hr after sunrise; Period 2: from the end of Period 1 to 3 hr before sunset; and Period 3: from 3 hr before sunset until sunset. No. = number of focal observations.

review in Paulus 1988), including geese that fed on waste grains (Raveling et al. 1972, Frederick and Klaas 1982, Davis et al. 1989). Geese spent more time resting during the mid-day. Increases in the time spent feeding in the morning and afternoon may compensate for the lack of feeding during the night. In addition, geese accumulate food in the esophagus when intake rates exceed processing rates (Owen 1972). A full gut may require geese to decrease the feeding rate and allow food to be processed, thereby influencing feeding patterns during the day.

The Influence of Season and Diet on Activities

Although no goose carcasses could be evaluated during this study to link behavior, body condition, and diet composition, Aleutian Canada geese exhibited similar seasonal behavior and diet patterns to other northern nesting geese (Wypkema and Ankney 1979, McLandress and Raveling 1981a,b, Gauthier et al. 1984, Ely and Raveling 1989, Alisauskas and Ankney 1992, Bromley and Jarvis, 1993, Gates et al. 2001). Winter diets were composed primarily of corn, particularly in the SJV, supplemented by green forage consisting of senescing pastures or sprouting winter wheat. During winter in the SJV, Dahl[3] (1995) found that pasture was the most available and most used habitat by Aleutian Canada geese in the SJV, but that corn was used in higher proportion

[3]Dahl, A.L. 1995. Diurnal habitat use by Aleutian and cackling Canada geese during winter in central California. Ph.D. Thesis, University of Washington, Seattle, Washington, USA.

compared to its availability. Geese typically used pasture and winter wheat fields for short periods in the morning before they moved into corn fields or during the mid-day while loafing near the roost site. Although high in energy content, corn may be deficient in certain essential amino acids, and geese may need to supplement their grain diet with green vegetation to acquire these necessary nutrients (Morrison 1951, McLandress and Raveling 1981a, Baldassarre et al. 1983, Jorde et al. 1983, Sedinger 1984). We speculate that the Aleutian Canada geese exhibited hyperphagia through intensive feeding on corn during the winter before beginning their spring migration northward.

Aleutian Canada geese move from the SJV to the NC in the spring prior to their departure to the breeding grounds (Woolington et al. 1979, Springer and Lowe 1998). We suggest that changes in habitat use and time allocation of Aleutian Canada geese from winter to spring are related to acquisition of nutrient reserves for migration to the breeding grounds and reproduction, similar to other northern-nesting geese (Wypkema and Ankney 1979, McLandress and Raveling 1981a,b, Gauthier et al. 1984, Madsen 1985, Ely and Raveling 1989, Alisauskas and Ankney 1992, Bromley and Jarvis, 1993, Gates et al. 2001). The geese switch from corn and pasture habitats in the SJV to strictly pasture in the NC and increase their time spent feeding. The spring increase in time allocated to feeding may be related to hyperphagia, an indication of forage energy and nutrient quality, or both. A switch to food resources higher in protein and deposition of protein reserves during spring has been found in other Canada goose subspecies (Raveling 1979a, McLandress and Raveling 1981a,b, Gates et al. 2001). Reserves gained during winter and on spring staging areas benefit geese on the breeding grounds by improving reproductive condition and increasing clutch size (Ankney and MacInnes 1978, Raveling 1979b). Subsequent research on Aleutian Canada geese should focus on evaluating body condition and energy and nutrient requirements through the nonbreeding season relative to habitat use and quality. With this information, a bioenergetic approach could be used to calculate the total energy and nutrient requirements of the desired Aleutian Canada goose population in specific locations, estimate the total energy and nutrient values available among various habitat types and qualities used by the geese, and then manage appropriate habitat acreages to meet their energy requirements.

We also believe that Aleutian Canada geese were not food-limited during this study. Closure zones prohibiting the hunting of all Canada goose subspecies were established in staging and wintering areas to prevent hunting mortality of Aleutian Canada geese through misidentification with other subspecies (Springer et al. 1978, Springer and Lowe 1998). Therefore, Aleutian Canada geese had relative freedom to access a diversity of foraging habitat throughout the hunting season. The unharvested corn knocked-down in stages at their terminal wintering area provided available grain forage adjacent to green vegetation and water roost sites.

Information presented here may provide a baseline for assessing behavioral changes as the population of this subspecies continues to increase and if land use patterns change in staging and wintering areas. Managers may also use this information in directing approaches to goose conservation. Recommendations include providing a diversity of grain and green forage to meet energy and nutrient requirements, perhaps

similar to the current approach using unharvested corn adjacent to pasture and day roosting sites in the SJV. Providing sufficient undisturbed areas for geese to meet their energy and nutrient requirements on the wintering and staging areas may be important to geese for reaching optimal body condition for migration and reproduction.

ACKNOWLEDGMENTS

Financial support was provided by the U.S. Fish and Wildlife Service (USFWS), Ecological Services Region 7, through the Washington Cooperative Fish and Wildlife Research Unit (WACFWRU), School of Fisheries, University of Washington. At the time of our study, the WACFWRU was supported by the USFWS (subsequently the National Biological Survey), the University of Washington, the Washington Departments of Ecology, Fisheries, Natural Resources, and Wildlife, and the Wildlife Management Institute. A. Dahl provided information and assistance and E. Harper, H. Mack, E. Rousseau, D. Shaw, and T. Thorn helped with field work. P. Springer, V. Byrd, B. Anderson, and other members of the Aleutian Canada Goose Recovery Team provided support throughout the project. L. Conquest, A. Shelly, and S. Zitser assisted with statistical analyses. D. Yparraguirre (California State Department of Fish and Game [CDFG]) and personnel of the Aleutian Islands Unit of the Alaska Maritime National Wildlife Refuge banded geese for the study. Numerous private landowners allowed the use of their property for this study and gave assistance. Housing, office space, and/or assistance were provided by E. Nelson, D. Wills, and D. Woolington (USFWS), D. Scott and K. Morse (California State Department of Parks and Recreation), C. Hampy and L. Depee (CDFG), and B. Funke and S. Fregien (WACFWRU). We thank several reviewers for their comments on earlier drafts of the manuscript.

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Received: July 21, 2001
Accepted: November 22, 2002

REFEREE ACKNOWLEDGMENTS

The following individuals have reviewed manuscripts for *California Fish and Game* during 2002. The list is as complete as possible. The editors apologize for any omissions and sincerely thank all those who have contributed to the quality of the journal by providing competent and timely reviews.

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